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No. 3

RELIQUIAE FARLOWIANAE

DISTRIBUTED FROM THE FARLOW HERBARIUM
OF HARVARD UNIVERSITY

ROLAND THAXTER

During a considerable period of years Dr. Farlow had been in the habit of setting aside from time to time, with a view to distribution for exchange, sets of New England Mosses, Hepatics, Lichens, and especially Fungi, of which somewhat over six centuries had accumulated at the time of his death. These had been largely collected and determined by himself, although a considerable number were contributed by other persons, especially by Mr. A. P. D. Piguet and Mr. A. B. Seymour. The Herbarium is now sending these sets to various botanical establishments in this country and in Europe, for purposes of exchange, and it has seemed desirable to publish this note concerning them as a matter of record and for the reason that, in a few instances, the names employed are new combinations or need some brief comment.

Each set comprises sixty decades, of which the first forty-five include only Fungi; while of those remaining, four decades are Lichens, five are Hepaticae, and six Musci. A certain number of additional specimens are also included in these sets, illustrating variations in hosts, imperfect conditions, etc., so that in all, each contains six hundred and ninety-three specimens. It may be mentioned in this connection that it is the intention of the Herbarium to send out, as they become available, in decades or in fascicles, further specimens, especially of the rarer Fungi, and including exotic as well as American species.

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The task of sorting, preparing, and labeling approximately twenty-five thousand specimens for this distribution has been considerable, and the Herbarium is under great obligations to Mr. Seymour, Mr. Piguet, and Miss Nickerson, of the Herbarium Staff, for the great amount of careful and painstaking work which has been necessary. Mr. Seymour has himself printed and revised the labels, an undertaking which of itself has been laborious, exacting, and time-consuming, and in his case to a large extent a labor of love for the purpose of forwarding the accomplishment of Dr. Farlow's original intentions.

The determinations of the species included in this set are almost wholly those made by Dr. Farlow, either personally or after submission to other experts, and in only a few instances has it been thought desirable to make slight changes, since the extent to which they represent his expert opinion as to identities forms perhaps the most important element of its value. It should be remembered, nevertheless, that some of these determinations may have been provisional in his mind, and subject to further verification or modification, had he been able to go over them for final revision before their distribution; and it is very probable that errors, which he would himself have corrected, may be thus perpetuated.

For the convenience of those who make a practice of binding their sets of exsiccata in preference to distributing them in the obliette of a General Herbarium, title pages and lists of each of the six volumes have been printed and distributed with the sets.

No. 15. *Diatrypella ciliatula* (Fr.) Farlow, nov. comb.

The *Sphaeria ciliatula* of Fries,¹ placed in *Calosphaeria* by Kars-ten and represented in the Farlow Herbarium by various collections from New England and Europe, appears to be rightly included in *Diatrypella*.

No. 73. *PLEOMASSARIA MAXIMA* Ell. & Ev.

The melanconaceous condition, *Sporidesmium Fusus* B. & C., is present in many of the specimens, some of which are over-mature. The material has been examined by Dr. Shear, who confirms the identity of this form with his *P. Magnoliae*.

¹ Syst. Myc. 2: 406. 1823.

No. 102, *a, b, c*. **CENANGIUM BALSAMEUM** Peck

The three specimens included comprise one ascigerous and two pycnidial stages, the latter *Gelatinosporium abietinum* Peck, formerly described as an imperfect stage of Peck's "var. *abietinum*" (Peck's Report 43: 86 (40), 1890). There seems to be no previous mention of its association with the type form.

No. 106. **CENANGIUM TURGIDUM** (Schw.) Fries

Mr. Seymour notes that, although this name is used in Dr. Farlow's label, the species seems to be a synonym of *Peziza quercna* Schw.² This, being the older specific name, should therefore have priority, and the species should thus bear the name **Cenangium querneum** (Schw.) Seymour.

No. 120. **GLOCLADIUM PENICILLIOIDES** Corda

This genus of Plectascineae, which was inadvertently included among the Discomycetes in assembling the sets, is familiar to any one who has dealt with laboratory cultures; often producing its perithecia on dung and other substances. In nature it may be pseudohypogaeous, occurring on buried decaying roots, and in the present instance was found growing away from the light in a pile of old seaweed used for fertilizer. I am myself responsible for the conclusion that *Penicillium insigne* Bainier, *Licipenicillium insigne* Brefeld, and *Lilliputia Gaillardii* Boud. & Pat. are synonyms, and am under the impression that there are still others.

No. 121. **GODRONIA NEMOPANTHIS** (Peck) Sacc.

An erratum in this label is "conidia" for "pycnidia." There appears to be no previous reference to the association of this species with a *Sphaeronema*.

No. 122. **Godronia turbinata** (Schw.) Farlow, nov. comb.

This is transferred by Dr. Farlow from the genus *Tympanis*, in which it was originally placed by Schweinitz.³ It is a conspicuous and characteristic form on *Diertrilla Lonicera* Mill., and has been

² Schr. Nat. Ges. Leipzig 1: 124. 1822.

³ Trans. Am. Phil. Soc. II. 4: 237. 1832.

collected at Chocorua, N. H., by Dr. Farlow, and in quantity by myself at Kittery Point, Maine.

No. 135, *a* and *b*. ***Pezicula pruinosa*** Farlow, nov. sp.

Cupulis cinnamomeis vel dilute vinaceo-cinnamomeis (Ridgway) sparsis vel seriatim erumpentibus, primum urceolatis vel subturbatis, breve stipitatis, basi albopruinosus; denique expansis disco plano pallidiore, .5-1 mm. lato: ascis 8-sporis, 95-110 x 18-21 μ : sporidiis oblique monostichis vel subdistichis, hyalinis, continuis, subellipticis vel subcymbiformibus, inaequilateralibus, utrinque rotundatis, 22-25 x 8-9 μ : paraphysibus filiformibus, copiosis, simplicibus vel apice subramosis, 1 μ diam.

Sharon and Cambridge, Mass.; Chocorua, N. H., on *Amelanchier*.

This is the perfect stage of the well-known and striking *Sphaeroma pruinosa* Pk.,⁴ with which it is not uncommonly associated on *Amelanchier* in the vicinity of Cambridge, although this association does not seem to have been previously recorded.

No. 144. ***Scleroderris Cephalanthi*** (Schw.) Farlow, nov. comb.

This species, placed in *Peziza* by Schweinitz,⁵ is here transferred for the first time by Dr. Farlow to *Scleroderris*.

No. 159. ***Aposphaeria brunneotincta*** Farlow, nov. sp.

Peritheciis majoribus, discretis vel subaggregatis, nigris vel nigrobrunneis, sphaericis vel irregularibus, siccatis saepe depressis vel collapsis, superficialibus vel basi insculptis, 250-500 μ diam., poro irregulari pertusis. Sporidiis minoribus 5-10 x 1.5-2.5 μ , cylindræis, suballantoideis vel subfusiformibus, rectis vel curvulis, brunnescentibus; sporophoris brevibus, fasciculatis, ramosis suffultis.

On the inner surface and along the sutures of chestnut burs, *Castanea dentata* (Marsh.) Borkh., Sharon, Mass. April, 1908. A. P. D. Piguet.

According to Dr. Farlow's memorandum, this species occurs in the Curtis Herbarium, under *Sphaeria*, with this specific name. Although Dr. Farlow is, responsible for this reference, it is with

⁴ Ann. Rep. N. Y. State Mus. 24: 85. Jan. 1872.

⁵ Schr. Nat. Ges. Leipzig 1: 123. 1822.

regret that I have felt obliged to be concerned in making an addition to so vague and uninteresting a genus.

No. 164, *a* and *b*. *COSTANTINELLA CRISTATA* Matruchot

As far as I am aware this is the first American record of this species. The Cambridge gathering (164 *a*) has been determined by myself and appears to correspond in all respects to the figures and description given by Matruchot of the type material, which he also found growing on dead leaves on the ground. Although he regards them as distinct, it seems not improbable that this species is not different from Bonorden's *Verticillium pyramidale*, with which it corresponds very closely in appearance, even to the peculiar sterile terminations of the main sporophores. The peculiar character on which the genus is based, namely, the crest-like origin of the spores on a curved "basidium," may well have escaped the notice of Bonorden, whose figures are manifestly diagrammatic.

It seems to me somewhat doubtful whether No. 164 *b*, which was regarded by Dr. Farlow as the same, should rightly be referred to this species. It occurs very commonly on rotten logs and on the inner side of moist loose bark. It forms a much thinner growth, without the cottony character of the type, and is a smaller plant. Although it has the same crest-like type of sporulation, it seems to lack the conspicuous and well-differentiated sterile terminations of the main sporophores above alluded to. Though a *Costantinella*, I should therefore feel some hesitation in regarding the two as belonging to a single species.

No. 469. *Calicium Rhois* (B. & C.) Farlow, nov. comb.

This is the *Stilbum Rhois* B. & C.* of the Curtis Herbarium. Whether the smaller *Calicium Curtisii* of Tuckerman should be regarded as distinct, I do not feel competent to judge.

No. 542. *SPHAGNUM CUSPIDATUM* Ehr. var.

Dr. A. LeRoy Andrews informs me that the form distributed is regarded as a distinct species under the name *S. Torreyanum* Sulliv.

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* Grevillea 3: 64. 1871.

NEW OR NOTEWORTHY RUSTS ON CARDUACEAE¹

H. S. JACKSON

In connection with a study of the species of *Puccinia* occurring on Carduaceae, which the writer has been making while preparing the manuscript of this group for the rust portion (Vol. 7) of the *North American Flora*, a number of undescribed species have come to light and certain interesting situations encountered.

The original plan to include such material in a series of papers dealing with the species on Carduaceae from all parts of the world² has not been abandoned, but owing to the difficulty of obtaining material of all the extra-limital species, and the prospect of early publication of the remaining numbers of the rust portion of the *North American Flora*, it has seemed best to record the following species and notes at this time.

Puccinia clara nom. nov.

Puccinia hyalina Jackson, Bot. Gaz. 55: 298. 1918. Not *P. hyalina* Dietel, 1905.

In 1918 the writer used the name *Puccinia hyalina* for a species on *Vernonia scariosa* Arn. from Ceylon. The above name is now offered as a substitute, since it has been found that the earlier use of *P. hyalina* by Dietel (cf. Engl. Bot. Jahrb. 37: 99. 1905) for a Japanese *Carex* rust had been overlooked.

Puccinia tonduziana Speg. Bol. Acad. Nac. Ci. Cordoba 23: 184. 1919

This species was described from material collected by A. Tonduz, September, 1896, on an unknown arborescent composite, near San Francisco, Costa Rica.

¹ Contribution from the Botanical Department of the Purdue University Agricultural Experiment Station.

² Cf. H. S. Jackson, Carduaceous Species of *Puccinia*.—I. Species occurring on the tribe Vernonieae. Bot. Gaz. 55: 289-312. 1918.

A specimen of the original collection, received some time ago by Dr. Arthur from Spegazzini, has been carefully studied and it is evident that the species is identical with *Puccinia praealta* Jackson & Holway (cf. Jackson, Bot. Gaz. 55: 306. 1918). The latter was described from several collections on *Vernonia triflosculosa* H.B.K. made by E. W. D. Holway in Guatemala and Costa Rica. A comparison of the host of *P. Tonduziana* with *P. praealta* leaves little doubt that they are the same.

Spegazzini, presumably on account of the character of the sorus, mistook the colorless uredospores for aeciospores, and described aecia and telia only for the species. His specimens are considerably older than most of the Holway collections and show some sori on the under surface of the leaves, while many of the epiphyllous sori are empty and their deep-seated origin is not as evident.

PUCCINIA SUBDECORA Sydow & Holway; Sydow, Ann. Myc. 1: 17.

1903

With this *Puccinia*, which occurs in the west on *Coleosanthus grandiflorus* (Hook.) Kuntze, an *Aecidium* is sometimes associated, and for a time it was thought that it was a long-cycled *auto-Puccinia*. When the final study of this species was made, however, the writer became convinced that the aecia belonged to a heteroecious rust, on account of the fact that no uredinia developed in certain collections on which the aecia were well past maturity, and because of differences in distribution. Ten aecial collections are in the Arthur herbarium from Colorado, Arizona, and New Mexico, while only five uredinial or telial collections have been made in Colorado and Utah.

A careful search was therefore made for evidence as to the type of life history of this species. A. O. Garrett made a uredinial collection of this species June 22, 1905, at Mill Creek Canyon, Salt Lake County, Utah. The sori in this collection are confined to the stems of young shoots and occur just below the surface of the ground. A careful study of this collection has revealed the presence of a few pycnia associated with these uredinia, indicating that this species is a brachy-form referable to the genus *Bullaria* of the Arthurian classification. With reference to this collection Mr.

Garrett wrote (in litt. Jan. 21, 1919): "I pulled up some of the plants of the *Coleosanthus* for another purpose and noticed the sori on the stems next the roots and entirely invisible from the surface of the ground." This observation, together with the finding of pycnia on the collection referred to, suggests that the life history of many more species of *Puccinia* could be determined if collections could be made early in the season as the plants are coming through the ground.

The aecia mentioned above have since been described as *Aecidium arcularium* Arth. (cf. Bull. Torrey Club 47: 478. 1920).

PUCCINIA KUHNIAE Schw.

A careful study of the common rust on *Kuhnia* in comparison with the species on closely related hosts has resulted in the conviction that *Puccinia Brickelliae* Pk. and *P. Barroetiae* Syd. should be considered synonymous with *P. Kuhniae*. The hosts of the three species are very closely related and there is no essential difference between the rusts. The determination of the life history of this species as a *brachy-Puccinia* is based entirely on cultures made by Dr. Arthur (cf. Jour. Myc. 12: 23. 1906 and Mycologia 1: 233. 1909), no field collections of pycnia associated with uredinia having been made.

The type locality for this species was recorded by Schweinitz as Bethlehem, Pennsylvania. Since this is a western rust, the most eastern locality of any recent collection being in Indiana, there is some doubt whether the type collection is from Pennsylvania as stated. It is possible that Schweinitz made this collection in Indiana, as it is known that at one time he traveled as far west as Hope, Indiana.

The synonymy, etc., of the species, according to this interpretation, is as follows:

PUCCINIA KUHNIAE Schw. Trans. Am. Phil. Soc. II 4: 296. 1832

Puccinia Brickelliae Peck, Bull. Torrey Club 12: 34. 1885.

Dicacoma Brickelliae Kuntze, Rev. Gen. 3¹: 468. 1898₁

Dicacoma Kuhniae Kuntze, Rev. Gen. 3¹: 469. 1898.

Puccinia Barroetiae Sydow, Monog. Ured. 1: 28. 1902.

Bullaria Kuhniae Kern, Trans. Am. Microsp. Soc. 32: 65. 1913.

ON CARDUACEAE [EUPATORIEAE]:

Barroetia sp., *Coleosanthus* (*Brickellia*) sp., *Kuhnia* sp.

TYPE LOCALITY: "Bethlehem, Pennsylvania," on *Kuhnia* sp., probably error for Indiana.

DISTRIBUTION: Indiana to Montana and Arizona, south to Texas and southern Mexico.

***Puccinia redempta* sp. nov.**

O. Pycnia unknown.

II. Uredinia hypophyllous, scattered or sometimes crowded and more or less confluent, roundish or elliptic, 0.5-1 mm. across, tardily naked, pulverulent, chestnut-brown, ruptured epidermis cinereous, conspicuous; urediniospores globose or ellipsoid, somewhat irregular, 23-27 by 26-32 μ ; wall dark cinnamon-brown, 1.5-2 μ thick, moderately echinulate, the pores 2, approximately equatorial.

III. Telia hypophyllous, scattered, roundish, 0.5-0.8 mm. across, tardily naked, pulverulent, chocolate-brown, ruptured epidermis cinereous, conspicuous; teliospores ellipsoid, somewhat irregular, 30-35 by 43-58 μ , rounded at both ends, slightly constricted at septum; wall chestnut-brown, 3-4 μ thick, slightly thickened at apex, 5-7 μ , concolorous or slightly lighter in color at apex, smooth; pedicel colorless, flexuous, short, deciduous or equalling the spore, often attached obliquely.

ON CARDUACEAE [EUPATORIEAE]:

Eupatorium atriplicifolium Lam., on bank, Road from town to Highbush, Tortola, West Indies, Feb. 13-17, 1913, N. L. Britton and J. A. Shafer, phan. spec. no. 705 (type).

The specimen on which this species is based is fairly ample and was obtained from a specimen in the phanerogamic herbarium at the New York Botanical Garden by the writer in 1917.

It belongs to the smooth-spored group of *Eupatorium* Puccinias and is apparently most closely related to *P. pachyspora* Diet. and *P. Eupatorii* Diet., differing from them both in the slightly thickened apex and from *P. Eupatorii* in the much broader spores. The urediniospores are not compressed laterally as in *P. pachyspora* and *P. Kuhniae* Schw.

PUCCINIA TOLIMENSIS Mayor, Mem. Soc. Neuch. Sci. Nat. 5: 516.

1913

This species of *micro-Puccinia* was described from a single collection made by E. Mayor on *Eupatorium* sp., near Soledad in the Central Andes, Department of Tolima, Colombia, Oct. 6, 1910 [No. 64]. Three collections were made by E. W. D. Holway in Guatemala, one on *Eupatorium pansamalense* Robinson (Holway 802) and two on *Eupatorium* sp. indet. (Holway 22,806).

On July 22, 1917, a collection of a short-cycled *Puccinia* was made by the writer, in company with H. H. Whetzel and E. F. Hopkins, on *Eupatorium urticaefolium* Reichard, in Bergen swamp, Genesee County, New York. After careful study it has been decided to assign this collection to the above-named species. The distribution, from central New York to Colombia, South America, in isolated localities, suggests that it should be found also in other places.

***Puccinia Parthenices* sp. nov.**

II. Uredinia not seen; urediniospores in the telia obovate or ellipsoid, 16–23 by 24–26 μ , slightly flattened laterally; wall light cinnamon-brown, 1.5–2.5 μ thick, very finely and closely echinulate, appearing smooth when wet, the pores 2, equatorial.

III. Telia hypophyllous, rarely epiphyllous, round, 0.4–0.8 mm. across, early naked, compact, pulvinate, blackish-brown, ruptured epidermis not conspicuous; teliospores obovate, oblong or ellipsoid, 20–26 by 32–45 μ , rounded or obtuse above, rounded below, slightly constricted at septum; wall light chestnut-brown, 1.5–2.5 μ thick, apex thickened 7–9 μ by a broad semi-hyaline umbo, similarly thickened over pore or lower cell at septum, smooth; pedicel colorless, firm, once to thrice length of spore.

ON CARDUACEAE [HELIANTHEAE]:

Parthenice mollis A. Gray, Ft. Lowell, Arizona, Oct. 24, 1903,

J. J. Thornber 1029, comm. L. N. Goodding (type); Bahoquevari Mts., Arizona, Oct. 24, 1919, L. N. Goodding 43.

This species was separated from specimens in the Arthur herbarium tentatively assigned to *P. Parthenii* Arth. It differs from that species as now interpreted in both urediniospore and teliospore characters. The urediniospores in *P. Parthenii* are globose or ellipsoid, 20–23 by 23–32 μ , with walls 3–3.5 μ thick, and the teliospores are ellipsoid, 28–32 by 38–48 μ , with walls 4–5 μ thick.

Puccinia Parthenii Arth. Bull. Torrey Club 37: 570. 1910

This name was based on *Uredo Parthenii* Speg., which was described in 1899 from a uredo on *Parthenium Hysterophorus* L. Telia were found by Dr. Arthur on two collections on *P. argentatum* A. Gray made by F. E. Lloyd in Mexico. With these collections were included one uredinial collection on *P. Hysterophorus* from Mexico State (Holway 3228) and one on *P. incanum* H.B.K. from Texas (Tracy & Earle 324a).

A recent study made by the writer has led to the conclusion that two distinct species were probably included. The urediniospores of the collection on *P. Hysterophorus* are quite different from those on *P. argentatum*. On the former they are obovate or triangular, 20-24 by 24-28 μ , with walls 1.5-2.5 μ thick, minutely and sparsely echinulate, the pores 3, one in apex and two subequatorial, while on the latter they are globose or ellipsoid, 20-23 by 23-32 μ , the walls 3-3.5 μ thick, finely and moderately echinulate, the pores 2 or 3, approximately equatorial.

Parthenium Hysterophorus, as noted above, is the type host for *Uredo Parthenii* Speg. Unfortunately this has not been seen, and it has not been possible to determine with certainty whether or not the uredinial collection made by Holway in Mexico is identical. It seems best, however, to exclude *Uredo Parthenii* Speg. from *Puccinia Parthenii* Arth. for the present and to tentatively assign to it the Mexican collection on *P. Hysterophorus*. The collection made by Lloyd at Mazapil, state of Zacatecas, Mexico, March 27, 1908, on *P. argentatum* should be taken as the type of *Puccinia Parthenii* Arth. as emended.

Puccinia additicia Jackson & Holway

This name was published by Dr. Arthur at our request as a substitute for the name *P. Corcopsidis* Jackson & Holway, which was based on a Guatemalan collection determined as on *Corcopsis mexicana* (DC.) Hemsl. It happened that the name *P. Corcopsidis* was used by Miss E. Wakefield for an entirely different rust (a *micro-Puccinia*) on *Corcopsis* from Uganda, tropical Africa, four months previously (cf. Bull. Misc. Inf. Kew 1918: 209. Aug. 1918).

Recently the writer had occasion to compare *P. additicia* with

P. Electrae Dietel & Holway and found that the two species are identical. *P. Electrae* was based on a collection made by E. W. D. Holway in Oaxaca, Mexico, the host for which was determined as *Electra Galeottii* A. Gray. The genus *Electra* DC. 1836 (not *Electra* Noron., or *Electra* Panz.) is now considered identical with *Coreopsis*. Furthermore, S. F. Blake (Cont. Gray Herb. N. S. 52: 55. 1917) has recently shown that *C. mexicana* and *Electra Galeottii* are both synonyms of *Coreopsis mutica* DC.

The following is the correct synonymy, etc., of the species:

Puccinia Electrae Dietel & Holway; Holway, Bot. Gaz. 31: 333.
1901

Puccinia Coreopsidis Jackson & Holway; Arth. Am. Jour. Bot. 5:
536. Dec. 1918; not *P. Coreopsidis* Wakefield, Aug. 1918.

Puccinia additicia Jackson & Holway; Arth. Bull. Torrey Club
48: 32. 1921.

ON CARDUACEAE [HELIANTHEAE]:

Coreopsis mutica DC. (*C. mexicana* Hemsl., *Electra Galeottii*
A. Gray), Oaxaca and Guatemala.

TYPE LOCALITY: Oaxaca, Mexico, on *Electra Galeottii*.

DISTRIBUTION: Southern Mexico and Guatemala.

***Puccinia turgidipes* sp. nov.**

II. Uredinia not seen; urediniospores in the telia, strongly compressed laterally, when viewed with pores in optical section, oblong, 16-18 by 26-29 μ , when in face view, subcircular, 24-27 by 26-29 μ ; wall dark cinnamon-brown, 2.5-3 μ thick, moderately and prominently echinulate, the pores 2, opposite and equatorial.

III. Telia amphigenous, scattered, round, small, 0.2-0.5 mm. in diameter, early naked, becoming pulverulent, blackish-brown, ruptured epidermis not noticeable; teliospores globoid or broadly ellipsoid, 30-32 by 32-38 μ , rounded at both ends, not constricted at septum; wall chestnut-brown, 3-4 μ thick, thickened at apex to 6 μ , as well as over pore of lower cell near septum, smooth; pedicel colorless, once to twice length of spore, with thick walls above, becoming abruptly inflated, 12-24 μ from point of attachment.

ON CARDUACEAE [HELIANTHEAE]:

Viguiera deltoidea Parishii (Greene) Vasey & Rose, Estrella
Mts. near Maricopa, Arizona, Oct. 30, 1919, L. N. Gooding 48.

This species is easily distinguished from all other Carduaceous rusts, which we have studied, by the strongly compressed character of the urediniospores and the inflation of the pedicels of the teliospores when wet.

The host was determined by Dr. S. F. Blake.

***Puccinia triannulata* (Berk. & Curt.) comb. nov.**

Uromyces triannulatus Berk. & Curt.; Berkeley, Grevillea 3: 56. 1874.

Puccinia mirifica Dietel & Holway; Dietel, Erythea 3: 79. 1895.

Caecomus triannulatus Kuntze, Rev. Gen. 3: 451. 1898.

Dicoma triannulatum Arth. Résult Sci. Cong. Bot. Vienne 346. 1906.

Through the courtesy of Dr. R. Thaxter, I have had the opportunity of examining a fragment of the type of *Uromyces triannulatus* Berk. & Curt. from the Curtis Herbarium at Harvard University. A second fragment was obtained from the Kew Herbarium by Dr. J. C. Arthur. Both bear the same number, 2270. The specimen from the Curtis Herbarium is labeled as follows: "*Uredo triannulata* B. & C. on *Borrchia frutescens* Santee Canal (?) S. C., June 1848. Ravenel 758." The specimen from Kew is labeled, "*Uromyces triannulatus* B. & C. in *Borrchia frutescens* Car. Inf."

An examination of these specimens leaves no doubt that *Uromyces triannulatus* was based on the uredinial stage of the species later described as *Puccinia mirifica* Dietel & Holway and now known to occur on *B. frutescens* from South Carolina, Florida, and Texas, and on *B. arborescens* from Florida, the Bahamas, and Bermuda.

Pycnia occur with the uredinia in several collections, leaving no doubt that this is a true *brachy-Puccinia* referable to the genus *Bullaria* in the classification proposed by Dr. Arthur.

PUCCINIA BALSAMORRHIZAE Peck

When preparing the manuscript of this species for the *North American Flora*, two points of interest were noted which seem worthy of record at this time.

A comparison of the type with that of *P. W'yethiae* Peck re-

sulted in the conclusion that there was no essential difference between the two. *Balsamorhiza* and *Wyethia*, the host genera of the two species, are very closely related, and the distribution of *P. Balsamorhizae* includes that of *P. Wyethiae*.

The life history of this species has been unknown; no collections of aecia have ever been made to our knowledge on either host. In May, 1919, the writer made a collection of uredinia on young leaves of *Balsamorhiza* sp. at The Dalles, Oregon, which, when studied, showed a few pycnia associated with the uredinia, which occurred in elongated groups along the petioles and the midribs of the leaves. The pycnia are few, gregarious, inconspicuous, orange-yellow, flask shaped, 70-100 by 100-130 μ , the ostiolar filaments projecting slightly. This indicates that the species is a *brachy-Puccinia* referable to the genus *Bullaria* of the classification proposed by Dr. Arthur.

Following is the full synonymy of this species as interpreted above:

PUCCINIA BALSAMORRHIZAE Peck, Bull. Torrey Club 11: 49. 1884

Trichobasis Balsamorhizae Peck, Bot. Gaz. 6: 276. 1881.

Uredo Balsamorhizae DeToni; Saccardo, Syll. Fung. 7: 842. 1882.

Trichobasis Wyethiae Peck, Bot. Gaz. 7: 45. 1882.

Puccinia Wyethiae Peck; Harkness, Bull. Cal. Acad. Sci. 2: 442. 1887.

Dicoma Balsamorhizae Kuntze, Rev. Gen. 3²: 468. 1898.

ON CARDUACEAE [HELIANTHEAE]:

Balsamorhiza sp., *Wyethia* sp.

TYPE LOCALITY: [Salt Lake City], Utah, on *Balsamorhiza macrophylla*.

DISTRIBUTION: Colorado, Utah, and Montana to British Columbia and California.

***Puccinia vaga* sp. nov.**

II. Uredinia hypophyllous, becoming somewhat amphigenous, scattered, round, small, 0.2-0.4 mm. in diameter, early naked, pulverulent, cinnamon-brown, ruptured epidermis conspicuous; urediniospores globoid or broadly obovoid, 21-24 by 23-26 μ ; wall

light cinnamon-brown, thin, $1-1.5 \mu$, moderately and prominently echinulate, the pores 2, opposite and equatorial.

III. Telia amphigenous, scattered, round, small, $0.2-0.5$ mm. in diameter, early naked, pulvinate, becoming somewhat pulverulent, blackish-brown, ruptured epidermis evident; teliospores broadly or narrowly ellipsoid, $23-26$ by $27-48 \mu$, rounded at both ends, slightly constricted at septum; wall reddish chocolate-brown, concolorous, medium-thick, $3-4 \mu$, slightly thicker above, $4-5 \mu$; pedicel colorless, about twice length of spore.

ON CARDUACEAE [HELJANTHEAE]:

Verbesina sp., Cuernavaca, Morelos, Mexico, Jan. 1908, E. W. D. Holway (type).

This species appears to differ sufficiently from other *Verbesina* rusts to warrant specific rank. It is perhaps most closely related to *Puccinia abrupta* Dietel and *P. Verbesinae* Schw. It differs from the former in the less thickened apex of the teliospores and in urediniospore characters. From the latter it differs in the concolorous teliospore wall and the thin-walled urediniospores.

The *Verbesina* rusts have proven to be a difficult group and further study based on more ample material will probably result in a realignment of some of the species. The following key will serve to indicate how the North American species have been separated for the *North American Flora*:

Telia only in the life history.	<i>P. ferox</i> D. & H.
Aecia or uredinia or both in life history.	
Teliospore-wall not over 7μ thick at apex.	
Telia early naked.	
Teliospore-wall lighter at apex, uredinial wall $1.5-2 \mu$.	<i>P. Verbesinae</i> Schw.
Teliospore-wall concolorous, uredinial wall $1-1.5 \mu$.	<i>P. raga</i> Jackson
Telia long covered by epidermis.	<i>P. irregularis</i> Dietel
Teliospore-wall more than 7μ thick above.	
Teliospores typically rounded below.	<i>P. abrupta</i> Dietel
Teliospores typically narrowed below.	
Teliospore-wall laminate.	<i>P. intralata</i> Jackson
Teliospore-wall not noticeably laminate.	<i>P. cognata</i> Sydow

COLEOSPORIUM ARNICALE Arth. and PUCCINIA NUDA Ellis & Ev.

Coleosporium Arnicae Arth., described in 1907, was based on a single collection made by W. N. Suksdorf in Falcon Valley, Wash-

ington, Oct. 30, 1901. The host was originally identified as *Arnica foliosa* Nutt., but interpreted by Arthur as *A. cana* Greene. No other collections of a *Coleosporium* on *Arnica* have since been received in this laboratory and there has been some doubt as to the validity of the species. A year or two ago the writer, while working in the mycological herbarium of the New York Botanical Garden, had occasion to examine the type specimen of *Puccinia nuda* Ellis & Ev. This was also described as occurring on *Arnica foliosa* and was collected by Suksdorf (No. 200) in the same locality July 30, 1885. On the herbarium sheet containing the specimen of *P. nuda* there is a second collection of rust on the same host made at the same place and date (Suksdorf, No. 199). Ellis at the time he studied these specimens evidently supposed that the latter collection bore the aecidium of *P. nuda*, since the manuscript sheet of the original description in Ellis's handwriting (pasted on the herbarium sheet with the specimens) included a description of the rust on this collection as an *Aecidium*. When he published *P. nuda*, however, Ellis omitted the aecial description or any mention of the second collection. An examination of this made recently shows that it is unquestionably the uredinia of a *Coleosporium* identical with the type of *C. Arnicae* Arth. and on the same host.

More recently the writer has had occasion to study in detail the type of *Puccinia nuda*. This species is also known only from the type locality and collection. A few days previously *Puccinia Hemizoniae* Ellis & Tracy had been studied and the close resemblance between the two species was at once noted. As a result of this study the conclusion was reached that they are identical, and that the host of *P. nuda* is probably not *Arnica*, but a species of *Madia*, *Hemizonia*, *Hemizonella*, or some close relative of these.

Puccinia Hemizoniae (including *P. Madiæ* Sydow) occurs on the same group of hosts as *Coleosporium Madiæ* Cooke, and on account of the conclusion just recorded with reference to the *Puccinia*, the possibility that *Coleosporium Arnicae* was identical with *C. Madiæ* at once suggested itself.

A comparison of the two species has resulted in the conviction that the former should be considered a synonym of the latter, and

the host, which is identical with the host for *Puccinia nuda*, is probably also *Madia*, *Hemizonia*, *Hemizonella*, or some close relative.

The synonymy, etc., of the two species, according to the interpretation above, is as follows:

COLEOSPORIUM MADIAE Cooke, Grevillea 7: 107. 1879

Stichospora Madiae Sydow, Ann. Myc. 2: 30. 1904.

Coleosporium Arnicae Arth. N. Am. Flora 7: 94. 1907.

ON CARDUACEAE [HELIANTHEAE]:

Anisocarpus, *Centromadia*, *Harpaecarpus*, *Hemizonia*, *Madaria*, *Madia*, *Zonanthemus*.

TYPE LOCALITY: Sierra Nevada, California, on *Madia Nuttallii*.

DISTRIBUTION: British Columbia to central California.

PUCCINIA NUDA Ellis & Ev., Jour. Myc. 3: 57. 1887

Puccinia Hemizoniae Ellis & Tracy, Jour. Myc. 7: 43. 1891.

Puccinia Lagophyllae Dietel & Holway; Dietel, Erythea 1: 250. 1893.

Dicoma Hemizoniae Kuntze, Rev. Gen. 3³: 469. 1898.

Dicoma nudum Kuntze, Rev. Gen. 3³: 469. 1898.

Puccinia Madiae Sydow, Monog. Ured. 1: 121. 1902.

ON CARDUACEAE [HELIANTHEAE]:

Calycadenia, *Hemizonia*, *Lagophylla*, *Madaria*, *Madia*.

TYPE LOCALITY: Falcon Valley, Washington, on "*Arnica foliosa*"; error for *Madia* (?) sp.

DISTRIBUTION: Washington to central California; also in South America.

PUCCINIA MELAMPODII Dietel & Holway

A group of short-cycled species of *Puccinia* occurring in subtropical regions of North America on a number of Carduaceous hosts of the tribe Heliantheae have proven to be very puzzling. These include especially the following:

P. Melampodii Dietel & Holway, on *Melampodium* from Guatemala and Morelos.

P. Synedrellae P. Henn., on *Synedrella nodiflora*, from the West Indies and Panama; also in South America.

- P. Zinniae* Sydow, on *Zinnia tenuiflora*, from Jalisco.
P. Diaziana Arth., on *Ximenesia encelioides*, from Coahuila.
P. Tridacis Arth., on *Tridax procumbens*, from Cuba.
P. Eleutherantherae Diet., on *Eleutheranthera ruderalis*, from the West Indies and Panama; also in South America.
P. Tetranthi Sydow, on *Tetranthus hirsutus*, from Haiti.

It will be noted that each one is known in North America on a single host species, and all are on separate genera. To these should be added unnamed forms on *Parthenium Hysterophorus* from southern Texas and on *Splanchthes oleracea* from Martinique. The latter might possibly be properly referred to *Puccinia Splanthicola* Mayor.

A careful comparison of these forms has failed to reveal any method by which they can be separated on a morphological basis and it has been decided to treat them as one species in the *North American Flora*. It is possible, indeed quite probable, that they are biologically distinct and may even have had, in part, an independent origin. It seems reasonable to suppose that collectively or independently they are correlated with one or more cyperaceous rusts occurring in the same region, which have aecia on these or related hosts, but the genetic connection of which has not yet been determined.

It should be pointed out that this species is very much like *P. Emiliae* P. Henn. (see p. 119), which occurs on members of the tribe Senecioneae with a similar distribution. It is also related to *Puccinia Silphii* Schw., which occurs on *Silphium* sp. in temperate regions, but which has somewhat narrower spores.

The synonymy, etc., is as follows:

- PUCCINIA MELAMPODII Dietel & Holway; Holway, Bot. Gaz. 24: 32. 1897.
Puccinia solida Berk. & Curt. Jour. Linn. Soc. 10: 356. 1869.
 Not *P. solida* Schw. 1839.
Puccinia Synedrellae Lagerh.; Sydow, Ured. 376, hyponym. 1890.
Puccinia Synedrellae P. Henn. Hedwigia 37: 277. 1898.
Dicoma cubense Kuntze, Rev. Gen. 3^a: 466. 1898.
Dicoma Synedrellae Kuntze, Rev. Gen. 3^a: 470. 1898.

- Puccinia Zinniae* Sydow, Monog. Ured. 1: 188. 1902.
Puccinia Diaziana Arth. Bot. Gaz. 40: 203. 1905.
Puccinia Tridacis Arth. Bull. Torrey Club 33: 516. 1906.
Dasyscypha Synedrellae Arth. Résult Sci. Congr. Bot. Vienne 347.
1906.
Puccinia Eleutherantherae Dietel, Ann. Myc. 7: 354. 1909.
Puccinia Tetranthi Sydow, Ann. Myc. 17: 33. 1919.
Microppuccinia Synedrellae Arth. & Jackson; Arth. Bull. Torrey
Club 48: 41. 1921.

ON CARDUACEAE [HELIANTHEAE]:

Hosts as above.

TYPE LOCALITY: Cuernavaca, Mexico, on *Melampodium* [*dicaricatum*].

DISTRIBUTION: Central Texas to Panama and the West Indies; also in South America.

Puccinia solida B. & C. is based on a collection by Charles Wright, 1856-1857, in "Cuba Orientale" on an unknown composite, now interpreted as *Eleutheranthera ruderalis*. *Dicoma cubense* is based on the same collection.

It is very probable that there are other forms in South America and possibly in similar regions in other parts of the world which should be included here. It has, however, been impossible, up to the present time, to bring together all the material which would be needed in making such a comprehensive study, and it should be recognized that the treatment as outlined above is tentative only.

***Puccinia Flaveriae* sp. nov.**

O. Pycnia unknown, probably not formed.

III. Telia amphigenous or caulicolous, gregarious on discolored spots, or extending for considerable distances on stems, round, small, 0.2-0.5 mm. in diameter, tardily naked, chestnut-brown, pulverinate, the caulicolous sori long covered by the cinereous epidermis, ruptured epidermis of foliicolous sori conspicuous; teliospores irregularly ellipsoid, clavate or cylindric, 15-19 by 32-50 μ , often bent to one side, rounded, obtuse or more or less acute above, rounded or narrowed below, not constricted at septum; wall light cinnamon-brown, 1.5-2 μ thick, much thicker above, 5-10 μ , smooth; pedicel one half length of spore or shorter, firm, colorless with base of spore.

ON CARDUACEAE [HELENIEAE]:

Flaveria campestris J. R. Johnston (*F. angustifolia* A. Gray),
Manhattan, Kansas, Sept. 15, 1893, M. A. Carleton (type).

The collection on which this species is based has been included with *Puccinia Asteris* Duby in the Arthur Herbarium, but it does not seem to be that species, and an attempt to assign it elsewhere with any degree of certainty has not been successful. It appears to be a *Micropuccinia* and there are no species on related hosts with which this can be logically placed. It differs from *P. Actinellae* in the irregular lighter-colored spores borne in sori which arise just below the epidermis and remain long covered. It is most nearly like a collection on *Hymenopappus carolinensis* (Lam.) Porter, which has been assigned to *P. Grindeliae* Pk.

PUCCINIA MILLEFOLII Fuckel

This species is known from a few collections on *Achillea Millefolium* L. from California, Montana, and Oregon, and one on *A. lanulosa* Nutt. from New Mexico. A careful comparison of this species, using both American and European material, has failed to reveal any morphological basis for separating this from *P. conferta* Diet. & Holway, which occurs on various species of *Artemisia* from North Dakota to northern Texas and westward to Washington and northern California, also in Europe. The hosts are closely related and there seems no good reason for keeping them separate for purposes of the *North American Flora*.

The synonymy is as follows:

PUCCINIA MILLEFOLII Fuckel, Jahrb. Nass. Ver. Nat. 23-24: 55.
1870

Puccinia conferta Dietel & Holway; Dietel, Erythea 1: 250. 1893.

Puccinia recondita Dietel & Holway; Dietel, Erythea 2: 128.
1894. Not *P. recondita* Rob. 1857.

Puccinia artemisiicola Sydow, Monog. Ured. 1: 14. 1902.

Dasyscypha conferta Arth. Résult Sci. Congr. Bot. Vienne 346.
1906.

Dasyscypha Millefolii Arth. Résult Sci. Congr. Bot. Vienne 347.
1906.

Micropuccinia conferta Arth. & Jackson; Arth. Bull. Torrey Club
48: 40. 1921.

Micropuccinia Millefolii Arth. & Jackson; Arth. Bull. Torrey Club
48: 41. 1921.

PUCCINIA EMILIAE P. Henn. Hedwigia 37: 278. 1898

Puccinia Emiliae, a typical *micro-Puccinia*, is based on a collection made by Dr. J. Urban in Jamaica on *Emilia sagittata* (Vahl) DC. It is also known on *E. sonchifolia* (L.) DC. and *Neurolaena lobata* (L.) R. Br., having a distribution from southern Florida, Panama, and the West Indies.

In 1907, Rev. J. M. Bates collected at Red Cloud, Nebraska, a short-cycled *Puccinia* on the cultivated *Calendula officinalis* L. and *Dimorphotheca cuneata* DC. This rust has since been collected on the former host at Guanabara, Cuba, by J. R. Johnston; Urbana, Illinois, by H. W. Anderson, and at New Castle, Indiana, by H. F. Dietz. The last collection was found on plants grown in the greenhouse, the others being garden collections. The rust had been tentatively assigned to *Puccinia recedens* Syd. in the Arthur Herbarium and the collection on *Dimorphotheca* was issued under that name in Bartholomew's North American Uredinales 1863.

Recently, while studying the short-cycled *Puccinias* of this group, the writer found that, while there was some variation in the collections on different hosts, there was no sharp distinction between *P. Emiliae* and *P. recedens*. The latter has slightly shorter spores with somewhat thicker walls than the former.

Puccinia recedens, however, is a northern rust occurring on *Senecio* species and having a range extending from southern New York to West Virginia along the Atlantic coast and across the continent to the mountains of Oregon and Alberta. This species is interpreted, on account of the morphology of the teliospores and host relationships, as a correlated species with *Puccinia (Diacoma) Eriophorii* Thüm., which has aecia on *Senecio* and telia on *Eriophorum* with a quite similar range in North America.

Puccinia Emiliae, on the other hand, is apparently native of subtropical regions. For these reasons it has been decided to keep the two species separate and to assign to *P. Emiliae* the collections

noted above on the cultivated hosts *Calendula* and *Dimorphotheca*. It is suggested that *P. Emiliae* is probably correlated with some species of subtropical cyperaceous *Puccinia* (several of which have been described), the aecial connection for which is as yet unknown.

The collections on *Dimorphotheca* and *Calendula* add another rust to the increasing list of diseases of floricultural crops, which may, under certain conditions, become of considerable economic importance. Since these hosts are annuals, propagated by seed only, it is not anticipated that the rust will prove as destructive as those occurring on hosts propagated by cuttings.

***Uredo abdita* sp. nov.**

II. Uredinia obscured by dense tomentum of host, apparently amphigenous, round or oval, large, 0.5–1.5 mm. in diameter, early naked, very pulverulent, chestnut-brown, ruptured epidermis not conspicuous; urediniospores usually considerably flattened laterally, with pores in face view globose or broadly ellipsoid, 26–29 by 26–32 μ , with pores in optical section oblong or narrowly ellipsoid, 20–24 by 26–32 μ ; wall chestnut-brown, thick, 2.5–3 μ , moderately but very finely echinulate, appearing smooth when wet, the pores 2, superequatorial.

ON CARDUACEAE [SENECIONEAE]:

Senecio Cineraria DC. (cultivated), Catalina Island, California, Aug. 1912, E. Bethel (type).

This species differs in pore characters and markings of the urediniospores from other *Senecio* rusts which we have been able to obtain for examination.

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DARK-SPORED AGARICS—II

GOMPHIDIUS AND STROPHARIA

WILLIAM A. MURKILL

The first article of this series, published in MYCOLOGIA for March, 1922, dealt with the species of *Drosophila*, *Hypholoma*, and *Pilosace* occurring in the temperate regions of eastern North America. I shall take up now two genera having an annulus, in addition to a fleshy stipe; and these may easily be distinguished by the following key:

Lamellae decurrent, waxy; veil glutinous; spores black. *Gomphidius*
Lamellae adnate or adnexed; veil membranous; spores
purplish-brown. *Stropharia*

GOMPHIDIUS Fries, Gen. Hymen. 8. 1836

This genus is distinguished by its glutinous veil; decurrent, waxy lamellae; and black, elongate spores. There are very few species and these occur mostly in temperate regions. The single tropical species, *G. jamaicensis*, is known only from Cinchona, Jamaica, at an altitude of 1,500 meters. *G. tricolor* occurs in California; *G. oregonensis* is abundant on the Pacific coast; and *G. tomentosus* is rare; the last two species being known only from the coastal region.

- | | |
|---|-------------------------|
| Pileus reddish-brown, not blackening; context yellow; stipe yellowish-brown. | 1. <i>G. viscidus</i> |
| Pileus purplish-brown or yellowish-brown, often black-spotted, but not blackening entirely; context white; stipe whitish. | 2. <i>G. glutinosus</i> |
| Pileus pale-brownish-red, becoming entirely black on drying; stipe white, becoming black. | 3. <i>G. nigricans</i> |
| Pileus dark-red, becoming blackish on drying; stipe vinous-red. | 4. <i>G. tricolor</i> |
| Pileus dull-brownish-pink, becoming black-spotted; stipe yellowish-brown. | 5. <i>G. maculatus</i> |
| Pileus dingy-pink; stipe pale-yellow. | 6. <i>G. flavipes</i> |
| Pileus whitish, sometimes tinged with red, becoming blackish at times; stipe whitish. | 7. <i>G. furcatus</i> |

1. *GOMPHIDIUS VISCIDUS* (L.) Fries, Epicr. Myc. 319. 1838*Agaricus viscidus* L. Sp. Pl. 1173. 1753.*Parvillus pubescens* Ellis, Bull. Torrey Club 6: 76. 1876.

Pileus fleshy, convex, umbonate, 3-8 cm. broad; surface smooth, viscid, reddish-brown, not blackening; context compact, yellow; lamellae much branched, long decurrent, especially with age, rather broad, subcrowded, reddish-brown, sometimes slightly blackened in old specimens; spores subcylindric to subfusiform, smooth, translucent, uniguttulate, brownish, $16-23 \times 5-8 \mu$; stipe cylindric or tapering below, pale-brown with abundant yellowish-brown tomentum when young, rhubarb-colored within, solid, 4-5 cm. long, 4-10 mm. thick; veil not evident.

TYPE LOCALITY: Sweden.

HABITAT: On the ground in pine woods.

DISTRIBUTION: Eastern United States, New York to Alabama; also in Europe.

ILLUSTRATIONS: Hussey, Ill. Brit. Myc. 2: pl. 24; Pat. Tab. Fung. 2: f. 656; Richon & Roze, Atl. Champ. pl. 23, f. 7-10; Schaeff. Fung. Bavar. pl. 55; Sow. Engl. Fungi pl. 105.

2. *GOMPHIDIUS GLUTINOSUS* (Schaeff.) Fries, Gen. Hymen. 8. 1836*Agaricus glutinosus* Schaeff. Fung. Bavar. Ind. 17. 1774.

Pileus fleshy, obtuse, 5-14 cm. broad; surface purplish-brown, often with black spots, sometimes yellowish-brown, never entirely blackening, glutinous; context white, soft, watery, with no distinctive odor; lamellae decurrent, forking, entire, easily separating, short, white to cinereous, sometimes dark-brown but not blackening, subcrowded, broad; spores dark-brown, smooth, fusiform, translucent, $17-23 \times 4-6 \mu$; cystidia cylindric; stipe cylindric or larger below, viscid, whitish, due to the dense coat of appressed fibrils, 4-9 cm. long, 8-15 mm. thick; veil heavy, glutinous, leaving an evident annulus.

TYPE LOCALITY: Bavaria.

HABITAT: On the ground in coniferous woods.

DISTRIBUTION: Northeastern North America; also in Europe.

ILLUSTRATIONS: Richon & Roze, Atl. Champ. pl. 23, f. 11-14; Ricken, Blätterp. Deutschl. pl. 3, f. 1; Schaeff. Fung. Bavar. pl. 36; Sow. Engl. Fungi pl. 7.

3. *GOMPHIDIUS NIGRICANS* Peck, Ann. Rep. N. Y. State Mus.

110. 1897

Pileus convex or nearly plane, 2.5-5 cm. broad; surface pale-brownish-red, covered with a tough gluten which becomes black in drying; context firm, whitish; lamellae distant, decurrent, some of them forked, white, becoming smoky-brown, black in the dried plant; spores oblong-fusoid, $15-25 \times 6-7.5 \mu$; stipe subequal, longer than the diameter of the pileus, glutinous, solid, at first whitish, especially at the top, soon blackish by the drying of the gluten, whitish within, slightly tinged with red toward the base, 3.5-6 cm. long, 4-8 mm. thick.

TYPE LOCALITY: Westport, New York.

HABITAT: Under pine trees.

DISTRIBUTION: New England to Tennessee; also in Europe.

ILLUSTRATION: *Atk. Stud. Am. Fungi* f. 50, 51.

Good specimens are at Albany, attached to a herbarium sheet. According to Peck, the entire plant is black when dry because of a blackening gluten which covers it.

4. *GOMPHIDIUS VINICOLOR* Peck, Ann. Rep. N. Y. State Mus. 51:

291. 1898

Pileus thick, fleshy, convex or nearly plane, 2.5-6 cm. broad; surface viscid, dark-red, becoming blackish on drying; lamellae distant, decurrent, olive-brown or blackish when mature; spores oblong-fusiform, smooth, smoky-brown to black, $12-14 \times 3.5-4 \mu$; stipe subequal, glabrous, solid, vinous-red, paler within, 3-6 cm. long, 4-8 mm. thick.

TYPE LOCALITY: Lake Mohonk, New York.

HABITAT: On the ground in coniferous or mixed woods.

DISTRIBUTION: Eastern United States, New York to Alabama; also in California.

Good type specimens are to be seen on a sheet at Albany. The California plants are larger and have spores measuring about $17.5 \times 5 \mu$. Kauffman refers a small Michigan plant to this species as a variety and says that it may be necessary to separate it specifically because of its smaller size and smaller spores.

25. *GOMPHIDIUS MACULATUS* (Scop.) Fries, Epicr. Myc. 319.
1838

Agaricus maculatus Scop. Fl. Carn. ed. 2, 2: 448. 1772.

Pileus solitary to subcespitose, fleshy, convex, 4-8 cm. broad; surface viscid, dull-brownish-pink, becoming black-spotted; context thick, white; lamellae short-decurrent, thick, branched, of medium width, distant, at first whitish, then blackening; spores narrowly ellipsoid, smooth, pale-brown under the microscope, $18-23 \times 8 \mu$; stipe short, firm, equal, pale-brown, often blackening above, covered with a yellowish-brown tomentum, especially toward the base, yellowish-red within, 4-5 cm. long, 6-8 mm. thick; veil not evident.

TYPE LOCALITY: Carniola.

HABITAT: Among moss or debris in moist woods, especially under larch trees.

DISTRIBUTION: New York and Michigan; also in Europe.

ILLUSTRATION: Kauffm. Agar. Mich. pl. 23.

Specimens collected by Bresadola and myself in the Tyrol were described by me while fresh as follows: "Pileus viscid, smooth, glabrous, rosy-isabelline, spotted with black and becoming darker; lamellae rosy-isabelline when fresh, becoming smoky, distant, venose-connected, adnate or slightly decurrent; stipe lemon-yellow at the apex and pale-lemon-yellow at the base, smooth, glabrous, equal, concolorous, blackening like the pileus. A totally different plant from *G. viscidus*."

G. stillatus Strass., mentioned by Peck in Report 27 as occurring in the Adirondacks, should probably be referred to this species. According to Kaufman, *G. gracilis* Berk. & Br. is also probably not distinct.

6. *GOMPHIDIUS FLAVIPES* Peck, Ann. Rep. N. Y. State Mus. 54:
153. 1901

Pileus convex or nearly plane, 2-2.5 cm. broad; surface viscid, minutely tomentose in the center, slightly fibrillose on the margin, dingy-pink; context white; lamellae arcuate-decurrent, distant, whitish; spores oblong-fusiform, $22-30 \times 6-8 \mu$; stipe equal or somewhat narrowed below and pointed at the base, solid, slightly fibrillose, whitish at the apex, elsewhere pale-yellow both externally and internally, 4-6 cm. long, 6-8 mm. thick.

TYPE LOCALITY: Westport, New York.

HABITAT: In mixed woods.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATION: Peck, Ann. Rep. N. Y. State Mus. 54: pl. 1, f. 1-4.

Specimens at Albany are small, black, and very unsatisfactory for comparison. According to Kauffman, this species may be a form of *G. maculatus*.

7. *GOMPHIDIUS FURCATUS* Peck, Bull. N. Y. State Mus. 5: 649. 1899

Pileus fleshy, convex or nearly plane, rarely somewhat umbonate, 2.5-5 cm. broad; surface glabrous, viscid, whitish, sometimes tinged with red, occasionally with blackish stains when old or becoming blackish when bruised; context white; lamellae thick, distant, decurrent, many of them forked, whitish, becoming sooty-brown; spores oblong or subfusiform, 15-20 x 6-8 μ ; stipe longer than the diameter of the pileus, rather slender, curved or flexuous, firm, solid, whitish, 3.5-7.5 cm. long, 3-6 mm. thick.

TYPE LOCALITY: Kasoag, New York.

HABITAT: Under or near tamarack trees in swamps.

DISTRIBUTION: New York.

Well represented at Albany by several good typical specimens on a sheet.

STROPHARIA (Fries) Quél., Champ. Jura Vosg. 110. 1872

Agaricus § *Stropharia* Fries, Monog. Hymen. Succ. 1: 409. 1857.
Geophila Quél. Ench. Fung. 111. 1886.

This rather large genus is distinguished by a fleshy stipe, adnate or adnexed lamellae, and the presence of an annulus, which last is somewhat uncertain at times because of its evanescent character. Several of the species grow on manure or manured ground and are widely distributed. The tropical species of this genus were treated in MYCOLOGIA for March, 1918, and the western species in MYCOLOGIA for November, 1912.

Pileus viscid or subviscid, glabrous, or slightly squamulose in two species.

Pileus ornamented with scattered, floccose scales.

Surface of pileus yellowish.

1. *S. distans*

Surface of pileus greenish.

2. *S. acuminata*

- Pileus glabrous, usually some shade of yellow.
 Pileus 1-5 cm. broad.
 Pileus decidedly umbonate. 3. *S. umbonatescens*
 Pileus pallid, pale-tan on the disk. 4. *S. anellariformis*
 Pileus not as above.
 Stipe rather short and thick.
 Stipe 6-7 mm. thick. 5. *S. melanosperma*
 Stipe 3-5 mm. thick. 6. *S. coronilla*
 Stipe rather long and slender.
 Stipe dry. 7. *S. siccipes*
 Stipe viscid.
 Pileus remaining hemispheric. 8. *S. semiglobata*
 Pileus more or less expanding. 9. *S. adnata*
 Pileus 4-15 cm. broad.
 Stipe nearly glabrous. 10. *S. caesiopora*
 Stipe conspicuously revolute-scaly. 11. *S. depilata*
 Pileus not viscid, glabrous, never squamulose.
 Surface of pileus whitish or yellowish.
 Parasitic on *Coprinus*. 12. *S. epimyces*
 Not parasitic in habit.
 Pileus 5-8 cm. broad. 13. *S. campestris*
 Pileus 2-5 cm. broad.
 Lamellae bluish-brown. 14. *S. caesifolia*
 Lamellae purplish-brown. 15. *S. bilamellata*
 Surface of pileus some shade of brown.
 Pileus 1-4 cm. broad.
 Pileus brown, very thin. 16. *S. tenuis*
 Pileus subcinamon-colored, fading to ochraceous. 17. *S. merdaria*
 Pileus rich-reddish-brown. 18. *S. subbadia*
 Pileus 5-15 cm. broad.
 Lamellae whitish when young. 19. *S. rugoso-annulata*
 Lamellae violet when young. 20. *S. elegans*

I. STROPHARIA DISTANS (Pers.) Morgan, Jour. Myc. 14: 75.
 1908

- Agaricus distans* Pers. Neues Mag. Bot. 1: 103. 1794.
Agaricus squamosus Pers. Syn. Fung. 409. 1801; not *A. squamosus* Schaeff. 1774.
Agaricus subcernuus Schum. Enum. Pl. Saell. 2: 255. 1803.
Stropharia squamosa Quéf. Champ. Jura Vosg. 337. 1872.

Pileus fleshy, thin, convex to plane, 3-7 cm. broad; surface subviscid to dry, with concentric, superficial, floccose scales, avella-

neous-isabelline, ochraceous on the umbo; lamellae adnate or sinuate, crowded, fuliginous at maturity, white on the edges; spores oblong-ellipsoid, pale-umbrinous under the microscope, opaque, $10-14 \times 6-7 \mu$; stipe slender, tough, stuffed or hollow, yellowish or ferruginous, squamose-villose below the annulus, 6-12 cm. long, 4-6 mm. thick; annulus ample, persistent, distant.

TYPE LOCALITY: Europe.

HABITAT: On the ground or humus in woods, fields, and gardens.

DISTRIBUTION: Northeastern United States, south to North Carolina, and west to Minnesota; also in Europe.

ILLUSTRATIONS: Berk. Outl. Brit. Fungol. pl. 10, f. 6; Cooke, Brit. Fungi pl. 553 (560); Lucand, Champ. Fr. pl. 190; Ricken, Blätterp. Deutschl. pl. 63, f. 1.

I have specimens from Romell and Bresadola and made a collection in Kew Gardens of a number of plants growing on a mixture of humus and manure. Peck's specimens at Albany collected by him in the Catskills agree with mine from Europe.

In his 44th Report, Peck mentioned specimens collected near Salamanca that were colored a beautiful orange-red, which he considered a variety of *Stropharia squamosa* and "apparently equivalent to *Agaricus thraustus* var. *aurantiacus* of Cook's Illustrations." There are also at Albany specimens collected in Indiana by J. M. Van Hook (No. 2558) with the following notes:

"Pileus 6 cm. broad, orange-rufous (Ridgway), dotted with few scattered, light-yellow scales, flesh white, slightly reddish immediately beneath cuticle, not viscid (at least when dry), fleshy, flesh thin near margin, thick at center, slightly umbonate. Gills becoming dark-seal-brown. Spores purple-brown, $5-7 \times 12-14 \mu$. Stipe equal, reaching 11 cm. long, somewhat tapering at base, above ring white and finely scaly upward, below ring darker colored with scales color of pileus. Ring complete. Stipe stuffed."

I have good specimens of the same variety collected at Kittanning, Pennsylvania, by Mr. Sumstine, and at Shingletown Gap, Pennsylvania, by Dr. Overholts (No. 3446). Accompanying the latter are the following notes:

"Pileus 4-8 cm. broad, convex then plane, 'zinc-orange' or 'orange-cinnamon' (Ridgway), sometimes radiate-rugose at the center and slightly umbonate, with 2 or 3 concentric rows of white appressed separable scales near the margin, these later disappearing, dry; margin at first appendiculate with

veil fragments; flesh whitish or somewhat concolorous, taste mild; gills medium-close or slightly distant, spotted, at first gray-slate color, later gray-black, squarely adnate or with a slight decurrent tooth, 4-8 mm. broad; stem long and slender, light-brown, pruinose above the annulus, with conspicuous white scales below, equal or slightly enlarged below, hollow, 8-15 cm. long, 3-6 mm. thick; annulus well developed, superior, becoming black above from the spores."

2. *Stropharia acuminata* (Scop.) comb. nov.

Agaricus acuminatus Scop. Fl. Carn. ed. 2, 2: 447. 1772.

Agaricus viridulus Schaeff. Fung. Bavar. Ind. 1. 1774.

Agaricus aeruginosus Curt. Fl. Lond. 70. 1788.

Stropharia aeruginosa Quél. Champ. Jura Vosg. 110. 1872.

Pileus gregarious or subcespitose, fleshy, convex to plane, subumbonate, 5-10 cm. broad; surface verdigris-green, then yellowish, covered with mucus, with separable viscid pellicle, sometimes dotted with scattered white scales, especially on the margin; context soft, whitish or tinged with blue; lamellae adnate or sinuate, rather broad, crowded, pallid to grayish, at length purplish-brown, whitish-flocculose on the edges; spores ovoid or ellipsoid, smooth, subhyaline with a faint yellowish-brown tint under the microscope, 7-10 x 4-5 μ ; stipe equal, hollow, viscid, scaly below the annulus, bluish, 5-8 cm. long, 5-12 mm. thick; annulus distant, rather evanescent.

TYPE LOCALITY: Carniola.

HABITAT: On the ground among leaves or in woods; also in fields in moist regions of Europe.

DISTRIBUTION: Rare from New England to South Carolina and west to California; abundant in Europe.

ILLUSTRATIONS: Bull. Herb. Fr. pl. 530. f. 1; Cooke, Brit. Fungi pl. 551 (555); Curt. Fl. Lond. pl. 309; Gill. Champ. Fr. pl. 132 (650); Hussey, Ill. Brit. Myc. 1: pl. 35; Pat. Tab. Fung. f. 231; Schaeff. Fung. Bavar. pl. 1; Sow. Engl. Fungi pl. 264; Trans. Wisc. Acad. Sci. 17: pl. 64.

This very attractive species is rare in the United States, but I have found it abundant in Sweden, England, and other parts of Europe.

3. *STROPHARIA UMBONATESCENS* (Peck) Sacc. Syll. Fung. 5:
1021. 1887

Agaricus umbonatescens Peck, Ann. Rep. N. Y. State Mus. 30:
41. 1878.

Pileus at first conic, subacute, then expanded and umbonate, gregarious, 1-2.5 cm. broad; surface smooth, glabrous, viscid, yellow, the umbo inclining to reddish; context thin, pallid, with a fetid odor; lamellae adnate to slightly decurrent, crowded, plane, broad, at length ventricose, whitish or gray to blackish-brown, with a slight olivaceous tint; spores ellipsoid, smooth, purplish-brown under the microscope, $15-19 \times 10 \mu$; stipe equal, slender, stuffed to hollow, pallid with a yellowish tint, 5-10 cm. long; annulus scanty, fugacious.

TYPE LOCALITY: Schenevus, New York.

HABITAT: On manure in pastures.

DISTRIBUTION: Massachusetts, New York, and Michigan; probably also in Europe.

ILLUSTRATIONS: Kauffm. Agar. Mich. *pl.* 51, *f.* 1; Trans. Wisc. Acad. Sci. 17: *pl.* 65, *f.* B. Compare Kalchb. Ic. Hymen. Hung. *pl.* 16, *f.* 2.

The real type of this species was collected at Schenevus. Certain other specimens so named at Albany are distinct. Sterling's specimens are wrongly named; Morris's, from Massachusetts, are correct. Kauffman says it is not infrequent in Michigan, having large spores and a rather fetid odor, and being near to *S. paradoxa* P. Henn. in shape. Harper suggests that it may be *Stropharia mamillata* Kalchb., a species published in 1874. I have specimens of this from Bresadola and they certainly look like our plant. Manure-inhabiting fungi have a way of getting about and turning up almost anywhere.

4. *Stropharia anellariformis* sp. nov.

Pileus thick, convex, obtuse, 2 cm. broad; surface viscid, smooth, not striate, pallid, pale-tan on the disk; lamellae decurrent, subdistant, broad, pale-tan to fuscous, with a purplish tint; spores broadly ellipsoid or ovoid, slightly apiculate, dark-purplish-brown under the microscope, $9-10 \times 7-8 \mu$; stipe subcylindric, larger toward the apex, atomaceous above, fibrillose below, dry, solid, concolorous, 4-5 cm. long, 2-3 mm. thick; annulus persistent, distant 1 cm. from the pileus.

TYPE LOCALITY: New Orleans, Louisiana.

HABITAT: On manure.

DISTRIBUTION: Known only from the type locality.

Type collected by F. S. Earle (43) on September 4, 1908. The species suggests *Anellaria fimiputris* and the spores resemble those of *Anellaria* and *Campanularius* in form but are lighter in color, staining the lamellae purplish-brown rather than black.

5. *STROPHARIA MELANOSPERMA* (Bull.) P. Karst. Bidr. Finl. Nat. Folk 32: 489. 1879

Agaricus melaspermus Fries, Epicr. Myc. 219. 1838.

Pileus fleshy, soft, convex to plane, obtuse, 3.5-4.5 cm. broad; surface smooth, glabrous, slightly viscid, often areolate, white, straw-colored on the disk; lamellae slightly adnexed, crowded, ventricose, pallid to cinereous, then violet-black; spores ovoid, fuscous, $10 \times 6 \mu$; stipe equal, glabrous, hollow, white, 4-6 cm. long, 6-7 mm. thick; annulus membranous, white.

TYPE LOCALITY: Europe.

HABITAT: On manure or manured ground in the open or partially shaded.

DISTRIBUTION: New England, New York, Texas, Costa Rica, etc.; also in Europe.

ILLUSTRATIONS: Bres. Fungi Trid. pl. 61; Cooke, Brit. Fungi pl. 536 (559); Pat. Tab. Fung. f. 555; Schaeff. Fung. Bavar. pl. 51; Quél. Champ. Jura Vosg. pl. 24, f. 3; Bull. Champ. Fr. pl. 540, f. 1.

Specimens so named are at Albany, collected by Burnham on lawns in Albany in August, 1905. Similar plants were found by me at Lake Placid, growing scattered under a white pine tree in the open, and I described them as follows: "Pileus semiglobose, 5 cm. broad; surface smooth, glabrous, dry when found, pure-white, becoming slightly yellow in spots on drying; context white, firm, eaten by snails; lamellae sinuate-adnate, crowded, plane, 3-4 times inserted, pure-white at first, notched on the edges; stipe equal, dry, apparently solid, fibrillose-scaly, finely frosted above the tiny, apical ring-trace, 7 cm. long, 7 mm. thick; veil slight, white, evanescent."

Specimens from Bresadola resemble *S. bilamellata* in general shape and have dark-colored lamellae with spores that are broadly ellipsoid, smooth, umbrinous under the microscope, reminding one of *Panacolus* in shape, slightly apiculate, about $10-12 \times 7-8 \mu$.

Bulliard's figures show the gills of young plants to be nearly white, becoming practically black when colored by the matured spores. He did not describe the species and I do not find it in DeCandolle's treatment of Bulliard's plants. Fries, according to Bresadola, confused it with Bulliard's *A. coronilla*. The original spelling was *A. melanospermus*, although practically every author using the name since Bulliard's time has abbreviated it to *A. melaspermus*. *A. bulbularis* Batsch has been called a synonym, but his figure is quite different from Bulliard's and shows no annulus at all.

6. STROPHARIA CORONILLA (DC.) Quél. Champ. Jura Vosg. 237.
1872

Agaricus coronilla DC. Fl. Fr. 2: 202. 1805.

Pileus hemispheric to convex, at length expanded, 2-4 cm. broad; surface glabrous, slightly viscid, smooth, whitish or ochraceous, even and whitish-floccose or appendiculate on the margin; context white, firm, with a slight, unpleasant odor; lamellae adnate or sinuate, rather broad, crowded, pallid to dark-violet and at length purplish-black, the edges whitish-fimbriate; spores ellipsoid or ovoid, smooth, violet-purple under the microscope, 8-12 x 4-6 μ ; stipe equal or slightly tapering upward, dry, smooth, white or slightly yellowish, solid to hollow, flocculose above the annulus, fibrillose below, becoming shining, 3-4 cm. long, 3-5 mm. thick; annulus distant, striate above, white, persistent.

TYPE LOCALITY: France.

HABITAT: On the ground in pastures, gardens, or woods.

DISTRIBUTION: Infrequent in the northeastern United States westward to Wisconsin and Kansas; also in Europe.

ILLUSTRATIONS: Bull. Herb. Fr. *pl.* 507, *f.* 1; Cooke, Brit. Fungi *pl.* 535 (558); Pat. Tab. Fung. *f.* 232; Ricken, Blätterp. Deutschl. *pl.* 63, *f.* 5; Trans. Wisc. Acad. Sci. 17: *pl.* 65, *f.* A.

EXSICCATI: Ellis & Ev. N. Am. Fungi 2511.

Peck thought his *S. bilamellata* might be this species. According to Kauffman, *S. melanosperma* is not very different; and Saccardo and Ricken say that *S. obdurata* is the same. Specimens collected by Bartholomew in Kansas appear to agree with authentic material from Bresadola and with specimens collected by me in Europe.

7. *STROPHARIA SICCIPES* P. Karst. Medd. Soc. Faun. Fl. Fenn. 9:
46. 1882

Pileus subfleshy, hemispheric to expanded, obtuse, orbicular, 2-3 cm. broad; surface glabrous, viscid, clay-white, yellowish on drying, even or pellucid-striate on the margin; lamellae adnate-subdecurrent, clay-colored to fuscous; spores ellipsoid, pellucid-brown, $12-15 \times 7-9 \mu$; stipe flexuous or strict, subfibrillose, flocculose above the annulus, dry, stuffed or hollow, pallid, 4-7 cm. long, 2 mm. thick; annulus incomplete, dry, distant, subfloccose or pruinose.

TYPE LOCALITY: Finland.

HABITAT: On manure or manured ground.

DISTRIBUTION: Northeastern United States westward to Minnesota; also in Europe.

ILLUSTRATIONS: Trans. Wisc. Acad. Sci. 17: pl. 66, f. D, E, & F; 18: pl. 18, f. I.

Peck described a variety of this species as *S. siccipes radicata* in Mus. Bull. 67: 37. 1903, based on long-radicate specimens collected by Earle in June in the New York Botanical Garden. Harper described and figured both the species and the radicate variety. Karsten considered it a form of *Stropharia semiglobata*.

8. *STROPHARIA SEMIGLOBATA* (Batsch.) Quél. Champ. Jura Vosg.
112. 1872

Agaricus semiglobatus Batsch, Elench. Fung. Contin. 1: 141.
1786.

Pileus fleshy, subglobose to hemispheric, not expanding, gregarious to subcespitose, 1-4 cm. broad; surface light-yellow, smooth, glabrous, very viscid when moist; context pallid, soft; lamellae adnate, very broad, white or olive-gray, soon clouded with the ripening spores; spores ellipsoid, smooth, purplish-brown, $12-18 \times 7-10 \mu$; cystidia on edges of lamellae $30-45 \times 3-4 \mu$; stipe slender, cylindric, light-yellow, smooth, viscid, 6-9 cm. long, 2-4 mm. thick; veil glutinous when moist, leaving an incomplete, superior ring.

TYPE LOCALITY: Germany.

HABITAT: On manure or manured ground in fields or open woods.

DISTRIBUTION: Throughout temperate North America and Europe, and at high elevations in the tropics.

ILLUSTRATIONS: Atk. Stud. Am. Fungi f. 30; Batsch, Elench. Fung. f. 110; Bull. U. S. Dept. Agr. 175: pl. 25, f. 2; Cooke, Brit. Fungi pl. 539 (567); Curt. Fl. Lond. pl. 194 (as *A. glutinosus*); Hard, Mushr. f. 260; Hussey, Ill. Brit. Myc. 1: pl. 39, f. 2; Mycologia 4: pl. 56, f. 3; Palmer, Mushr. Am. pl. 12, f. 3, 4; Pat. Tab. Fung. f. 234; Ricken, Blätterp. Deutschl. pl. 63, f. 2; Sow. Engl. Fungi pl. 248; Trans. Wisc. Acad. Sci. 18: pl. 18, f. A-H.

A very common and easily recognized species. The spores vary considerably in size. Harper says there is a sterile form which differs only in having the gills white, unchanging, because there are no spores to blacken them. He gives an illustration of it.

9. *Stropharia adnata* (Huds.) comb. nov.

Agaricus adnatus Huds. Fl. Angl. ed. 2, 619. 1778.

Agaricus stercorarius Schum. Enum. Pl. Saell. 2: 286. 1803;
not *A. stercorarius* Bull. 1781.

Stropharia stercoraria Qué. Champ. Jura Vosg. 112. 1872.

Hypholoma peccosense Cockerell. Jour. Myc. 10: 108. 1904.

Pileus solitary or gregarious, hemispheric to expanded, 2-5 cm. broad; surface smooth, glabrous, viscid, often cracking on drying, whitish or some shade of light-yellow, margin even; context soft, white or yellowish, slightly bitter; lamellae adnate with decurrent tooth, very broad, crowded, white to brownish or greenish-black, whitish-flocculose on the edges; spores smooth, elongate-ellipsoid, violet-purple under the microscope, blackish-brown in mass, 16-20 x 10-12 μ ; stipe elongate, equal or enlarged at the base, stuffed to hollow, subviscid, flocculose-scaly below the annulus, pruinose above, 8 cm. or more long; annulus distant, slight, evanescent.

TYPE LOCALITY: England.

HABITAT: On manure.

DISTRIBUTION: Temperate regions of North America; also in Europe.

ILLUSTRATIONS: Cooke, Brit. Fungi pl. 538 (566); Trans. Wisc. Acad. Sci. 17: pl. 67.

Similar to *S. semiglobata* in habit and appearance, but gills becoming brownish-black or greenish-black instead of cloudy-black, and spores usually lighter in color, appearing olivaceous under a microscope. The cap is also not so persistently hemispheric as in

S. semiglobata. The two species approach each other very closely at times.

10. *STROPHARIA CAESIOSPORA* Kauffm. *Mycologia* 9: 166. 1917

Pileus convex, obtuse, firm or slightly elastic, gregarious, 4-9 cm. broad; surface chamois to honey-yellow (Ridg.), subviscid, even; margin somewhat crenate-lobed; context white, rather thick and compact, thin on the margin; lamellae crowded, narrow, adnexed-emarginate, at length rounded behind, heterophyllous, drab to hair-brown or ashy-gray; spores minute, ovoid, smooth, with a purplish-cinereous tint under the microscope, ashy in mass with a tint of purple, $5-6 \times 3-4 \mu$; stipe equal or slightly bulbous at the base, whitish, slightly lacerate above the annulus, stuffed to solid, fibrillose-glabrescent, 4-9 cm. long, 6-12 mm. thick; annulus persistent, membranous, flocculose below, striate-ridged above, becoming gray from the spores.

TYPE LOCALITY: Elkmont, Tennessee.

HABITAT: On the ground among debris in chestnut and conifer mixed woods.

DISTRIBUTION: Found several times in the vicinity of Elkmont.

11. *STROPHARIA DEPILATA* (Pers.) Sacc. *Syll. Fung.* 5: 1012. 1887

Agaricus depilatus Pers. *Syn. Fung.* 408. 1801.

? *Stropharia Hardii* Atk. *Jour. Myc.* 12: 194. 1906.

Pileus solitary or gregarious, convex to plane, obtuse, 4-15 cm. broad; surface glabrous, viscid, livid-yellow to cinnamon; margin even, often appendiculate; context firm, whitish, with somewhat disagreeable taste and no odor; lamellae rather crowded, adnate-decurrent, broad, white to purplish-black; spores ellipsoid, smooth, dark-gray with a purplish tint under the microscope, $9-14 \times 5-8 \mu$; stipe equal, solid to hollow, revolute-scaly below the annulus, floccose-scaly above, white to pale-yellow, 6-20 cm. long, 1-1.5 cm. thick; annulus distant, ample, scaly, white, persistent.

TYPE LOCALITY: Europe.

HABITAT: On much-decayed wood or humus in woods.

DISTRIBUTION: Northeastern United States westward to Michigan; also in Europe.

ILLUSTRATION: *Trans. Wisc. Acad. Sci.* 17: pl. 62, 63.

Specimens from Bresadola and Romell are in the Garden herbarium. Plants collected by me late in August on humus under a pine log in Maine, where I obtained several collections, had a "pale, dull-yellow cap, which was viscid when fresh; white, appendiculate margin; stipe and edges of gills pure-white." I also found it twice in deep, rich woods in the Adirondacks. Peck's specimens were at first referred to *Agaricus Hornemanni*, which was Fries's name for this species before he adopted that of Persoon. *Stropharia Hardii*, according to Harper, is probably this species, although the spores are described as smaller. I have not seen the types.

12. *STROPHARIA EPIMYCES* (Peck) Atk. Plant World 10: 128.
1907

Panaeolus epimyces Peck, Ann. Rep. N. Y. State Mus. 35: 133.
1884.

Stropharia coprinophila Atk. Jour. Myc. 8: 118. 1902.

Pileus fleshy, at first subglobose, then convex to expanded, 2-6 cm. broad; surface white, then dingy, silky-fibrillose; context soft, white or whitish, with mild odor and taste; lamellae adnexed, rounded behind, somewhat crowded, dingy-white, becoming brown or blackish, with white edges; spores ellipsoid, smooth, dark-purplish-brown under the microscope, almost black in mass, $7-8.5 \times 4-6 \mu$; cystidia clavate or subventricose, on a slender stalk, $40-60 \times 10-14 \mu$; stipe short, stout, tapering upward, strongly striatulate and minutely mealy or pruinose, solid in the young plant, hollow in the mature plant, but with the cavity small, white-annulate near the base from the white, floccose veil, 2.5-7 cm. long, 5-15 mm. thick.

TYPE LOCALITY: North Greenbush, New York.

HABITAT: Parasitic in groups on *Coprinus comatus*, *C. atramentarius*, and perhaps other species of the genus.

DISTRIBUTION: Northeastern North America, Canada to New York and west to Minnesota; perhaps also in Europe.

ILLUSTRATIONS: Plant World 10: f. 22-24; Hard. Mushr. f. 227; Jour. Myc. 2: pl. 80; Mycologia 8: pl. 178, f. C, D; pl. 179, f. A, B.

Interesting studies have recently been made of this rather queer species by Harper, Atkinson, Kauffman, and McDougall. Harper

calls attention to Lanzi's figures of *Pilosace algeriensis* as closely resembling our plant. Kauffman, as well as McDougall, says our plant is not a *Pilosace*, and he keeps it in *Stropharia* where Atkinson placed it. Specimens growing on *Coprinus comatus* were sent me in 1915 by Mr. Boughton, of Pittsford, New York, but they were not in good shape for study. My notes on them read: "Pileus cream-colored, 6 cm. broad; context white, taste mild; lamellae like those of *Agaricus campestris* in appearance; stipe white, 5 cm. long, 1.4 cm. thick. Not a *Panaeolus*, but like *Agaricus* without a ring." These would seem to agree with Harper's latest conclusions, but not with McDougall's.

13. *Stropharia campestris* Peck ms.

Pileus convex to plane or nearly so, gregarious, 5-8 cm. broad; surface smooth, moist when fresh, yellowish-white or cream-colored, becoming darker on drying; context compact, yellowish-white, with farinaceous or slightly bitter taste; lamellae thin, adnate, slate-colored tinged with violaceous, becoming blackish-brown tinged with purple; spores ellipsoid, purplish-brown, 10-12 x 6-8 μ ; stipe equal or slightly bulbous at the base, solid, annulate, white, 2.5-5 cm. long, 4-10 mm. thick.

TYPE LOCALITY: Morrisville Island, Pennsylvania.

HABITAT: On grassy ground.

DISTRIBUTION: New York and Pennsylvania.

According to Mr. Sterling, the bitter taste is destroyed by cooking and the mushroom is edible and better in flavor than *Agaricus campester*, for which it is sometimes mistaken and from which it may be separated by its adnate, not free, gills. The gills are at first concealed by the white veil, which finally ruptures and adheres partly to the margin of the pileus and partly to the stem. It is closely related to *Stropharia cacsifolia*, from which it differs in the color of the gills and possibly in flavor.

The above description and notes made by Dr. Peck were kindly furnished me by Dr. House. The type of this species was collected in August, 1905, by E. B. Sterling. I also have plants collected by L. M. Underwood on the Columbia Campus in October, 1899.

14. *STROPHARIA CAESIFOLIA* Peck, Bull. Torrey Club 22: 489.
1895

Pileus convex, 2.5-5 cm. broad; surface glabrous, white or whitish, sometimes brownish on the disk; lamellae close, rounded or emarginate behind, light-blue becoming dingy-bluish-brown; spores subellipsoid, $10-12.5 \times 6-7.5 \mu$; stipe equal or slightly thickened at the base, solid, glabrous, white or whitish, 2.5-4 cm. long, 4-6 mm. thick; annulus white.

TYPE LOCALITY: Rockport, Kansas.

HABITAT: In low sandy pastures.

DISTRIBUTION: Known only from the type locality.

A portion of the type is in the Garden herbarium. Bartholomew remarks that this species is much like the common mushroom, except that its gills have a fine light-blue color instead of pink. In the dried specimens they are dingy-grayish-blue, inclining to brown.

15. *STROPHARIA BILAMELLATA* Peck, Bull. Torrey Club 22: 204.
1895

Pileus fleshy, convex, becoming nearly plane in large plants, obtuse, 2.5-5 cm. broad; surface even, whitish or yellowish, glabrous; context pure-white; lamellae thin, close, adnate, purplish-brown in mature plants; spores ellipsoid, purplish-brown, $10 \times 5-6 \mu$; stipe commonly short, solid, sometimes hollow in large plants, white, annulate, 2.5 cm. long, 6-8 mm. thick; annulus well-developed, pure-white, striately lamellate on the upper edge.

TYPE LOCALITY: Pasadena, California.

HABITAT: In grass in streets or in cultivated fields.

DISTRIBUTION: New York to Alabama; also in California.

ILLUSTRATION: Bull. N. Y. State Mus. 122: *pl.* 112, *f.* 5-10.

Described from California, but found also at a few places in the eastern United States. Mr. B. C. Williams collected it at Newark, New York; Braendle at Washington, D. C.; Coker at Chapel Hill, North Carolina; and Earle at Auburn, Alabama. When Peck received Braendle's specimens, he revised his description. The species resembles *S. coronilla*.

16. *Stropharia tenuis* sp. nov.

Pileus convex, subumbonate, thin, 2.5 cm. broad; surface dry, with delicate, floccose patches, faintly striate, brown; lamellae ad-

nexed, crowded, of medium width, subconcolorous; spores broadly ellipsoid, obtuse at both ends, smooth, dark-purplish-brown under the microscope, $7 \times 5 \mu$; stipe slender, fragile, tapering upward, enlarged at the base, glabrous, silky, hollow, concolorous but slightly paler, 7 cm. long, 2-3 mm. thick; annulus distant 2.5 cm. from the pileus, ample, persistent.

TYPE LOCALITY: Chalmitte, New Orleans, Louisiana.

HABITAT: On the ground in wet woods.

DISTRIBUTION: Vicinity of New Orleans, Louisiana.

Collected by F. S. Earle, No. 116 (type). September 8, 1908; also on September 7, 1908, No. 101. A thin, fragile plant resembling certain species of *Drosophila*, but having an ample, persistent annulus. The color of the pileus in dried specimens varies from avellaneous to umbrinous or fuliginous; the stipe and annulus being nearly white.

17. STROPHARIA MERDARIA (Fries) Quél. Champ. Jura Vosg.

III. 1872

Agaricus merdarius Fries, Syst. Myc. 1: 291. 1821.

Pileus gregarious, convex to plane, obtuse, 3-4 cm. broad; surface glabrous, moist, hygrophanous, becoming striatulate, subcinnamon-colored when moist, ochraceous when dry; lamellae adnate, broad, yellowish to umbrinous; spores globose to ellipsoid, brownish-black, $12-17 \times 6-9 \mu$; stipe tough, short, stuffed or hollow, dry, flocculose, pallid, 2.5 cm. or more long; annulus lacerate, fugacious; veil often appendiculate.

TYPE LOCALITY: Sweden.

HABITAT: On manure.

DISTRIBUTION: North central United States; also in Europe.

ILLUSTRATIONS: Cooke, Brit. Fungi pl. 537 (565); Fries, Ic. Hymen. pl. 130, f. 3; Lucand, Champ. Fr. pl. 130; Ricken, Blätterp. Deutschl. pl. 66, f. 1.

I have excellent material collected by Romell and myself in Sweden, in which the spores are elongate-ellipsoid, smooth, opaque, yellowish under the microscope, reaching $17 \times 9 \mu$. Harper describes and figures what he considers *S. submerdaria* Britz., and says that Morgan refers it to *S. merdaria* as a variety. Kauffman finds this species in Michigan and follows Karsten in placing it in *Psilocybe*, since the stipe is described as tough.

18. *Stropharia subbadia* sp. nov.

Pileus rather fleshy, convex to nearly plane, solitary or gregarious, 1-2 cm. broad; surface smooth, dry, rich-reddish-brown, lighter on the margin, which is not striate, covered with an evanescent yellowish tomentum when young; lamellae sinuate, sub-ventricose, not crowded, rather broad for the size of the plant, whitish to dark-cinereous, at length purplish-brown, entire and whitish on the edges; spores ellipsoid, smooth, pale-purplish-brown under the microscope, about $7.5-8.5 \times 5.5 \mu$; stipe short, of medium thickness, equal, fibrillose-scaly, especially below, tawny-white, 2-3 cm. long, 2-3 mm. thick; veil slight, white, mostly becoming distributed along the stipe instead of forming a definite annulus.

TYPE LOCALITY: Auburn, Alabama.

HABITAT: On the ground in dry pastures.

DISTRIBUTION: Vicinity of Auburn, Alabama.

This may belong to *Drosophila*; a study of fresh plants is needed. Dried specimens suggest dried specimens of *S. coronilla*, but are differently colored and lack the ample, persistent annulus. The types were collected by F. S. Earle on October 16, 1900. Also collected by him on October 14, 1900, near the type locality in a close-cropped pasture of Bermuda grass.

19. *Stropharia rugoso-annulata* Farlow ms.

Pileus fleshy, hemispheric to convex, 5-15 cm. broad; surface glabrous or at times slightly and innately fibrillose on the margin, chestnut-colored, becoming paler on drying; context firm, thin, whitish, with mild taste; lamellae thin, crowded, wider than the thickness of the pileus, adnate, whitish when young, becoming dark-brown or almost black with age; spores ellipsoid, dark-brown, $10-12 \times 6-8 \mu$; stipe equal or slightly tapering upward, spongy within, sometimes becoming hollow with age, whitish, silky-fibrillose, with mycelium at the base at times, 5-8 cm. long, 10-12 mm. thick; annulus whitish, appearing double, the lower membrane radiately splitting on the margin.

TYPE LOCALITY: Newton, Massachusetts.

HABITAT: Rich, cultivated grounds.

DISTRIBUTION: Massachusetts.

Two collections are at Albany, one from George E. Morris and the other from G. B. Fessenden. I have specimens collected by Morris in a corn field at Waban, Massachusetts, September 13,

1905. The descriptive notes were kindly supplied in manuscript by Dr. House.

20. *Stropharia elegans* sp. nov.

Pileus fleshy, convex to plane, upturned at the margin in dried specimens, solitary, 5-10 cm. broad; surface dry or slightly moist, nearly smooth, glabrous, subshining, umbrinous, tinged with light-brown in younger stages, becoming isabelline-ochraceous-melleous at maturity; context white, very thin, except at the center, without characteristic odor, taste mild and peculiar, like some bulbs; lamellae adnexed, arcuate, crowded, rather narrow, entire and concolorous on the edges, dark-smoky to dark-violet, at length purplish-fuliginous; spores ovoid, smooth, umbrinous under the microscope, about $10-12 \times 7-8 \mu$; stipe slender, tapering decidedly upward from a bulbous base, glabrous, solid, white, smooth, and shining above the annulus, cream-colored below and longitudinally striate just below and near the annulus. 10-12 cm. long, 2-3 cm. thick at the base, 5-10 mm. thick at the apex; annulus large, membranous, white or slightly yellowish, fixed, distant about 3 cm. from the pileus, lobed on the margin.

TYPE LOCALITY: New York Botanical Garden, New York City.

HABITAT: In rich, low, partly shaded soil.

DISTRIBUTION: Known only from the type locality.

Collected on September 12, 1912, by Miss Mary E. Eaton and drawn in color by her. She found larger specimens at the same spot on September 16, 1912. A very beautiful plant, with brownish-umber cap, dark-violet gills, and a yellow stipe which tapers upward decidedly from a bulbous base.

DOUBTFUL AND EXCLUDED SPECIES

Stropharia albocyanca (Desmaz.) Quél. Champ. Jura Vosg. 236. 1872. According to Harper, this species occurs with us, being smaller than *S. aeruginosa* and having a white, dry stipe. Morgan referred to it as *S. pseudocyanca* (Letell.). Peck's specimens so named, from North River, New York, and those collected by Simon Davis at North Bethlehem, New Hampshire, differ from each other and from Bresadola's specimens.

Stropharia albonitens (Fries) Quél. Champ. Jura Vosg. 3: 11. 1875. Reported from Michigan by Kauffman, who says that it

may be known by the gray color of the gills and the yellowish tint on the stem in age.

Agaricus (Stropharia) Feildeni Berk. Jour. Linn. Soc. 17: 14. 1880. Collected on Bellot Island, Greenland, by Captain Feilden. The description is inadequate and I have not seen the type. Miss Wakefield, however, has kindly examined it for me and writes as follows:

"The type consists of one specimen about 6 cm. across in very bad condition. There is practically no stalk, only a mass of soil beneath. It gives one the impression of having been a dwarf, abnormal form. The upper surface of the pileus is also much covered with soil, so that one can judge little about it. The gills, as much as one can see of them, are very short. If it were ever found again the spores might serve to identify it. They are almost globose, and rather large, $7-9 \times 7-8 \mu$."

Stropharia Howcana (Peck) Sacc. Syll. Fung. 5: 1026. 1887. (*Agaricus Howcans* Peck, Bull. Buffalo Soc. Nat. Sci. 1: 53. 1873.) See *Pholiota Howcana* Peck, Bull. N. Y. State Mus. 122: 147. 1908.

Stropharia irregularis Peck, Bull. Torrey Club 27: 16. 1900. An annulate form of *Drosophila appendiculata*.

Stropharia Johnsoniana Peck, Ann. Rep. N. Y. State Mus. 41: 84. 1888. (*Agaricus Johnsonianus* Peck, Ann. Rep. N. Y. State Mus. 23: 98. 1872.) See *Pholiota Johnsoniana* Peck, Bull. N. Y. State Mus. 122: 147. 1908.

Stropharia micropoda Morg. Jour. Myc. 14: 73. 1908. Described from specimens growing on rotten wood at Preston, Ohio. Stover suggests that it may not be distinct from *Gymnopilus polychrous*.

Stropharia obturata (Fries) Quel. Champ. Jura Vosg. 110. 1872. (*Agaricus obturatus* Fries, Syst. Myc. 1: 283. 1821.) Reported from Illinois on the basis of a photograph taken by W. S. Moffatt. According to some, the species is not distinct from *S. coronilla*. Peck's specimens so named appear to belong in *Pholiota*.

Stropharia Schraderi Peck, Bull. Torrey Club 32: 80. 1905. Described from specimens collected by F. F. Schrader in sandy, grassy soil about stumps at Washington, D. C. The types have been examined and the species appears to me to belong in *Pholiota*.

Stropharia umbilicata Peck, Bull. N. Y. State Mus. 167: 49. 1913. Described from specimens collected among chips and sawdust in Minnesota. The types at Albany resemble *S. aeruginosa* in some ways, but are probably *Gymnopilus polychrous*, since specimens from New York called *S. umbilicata* by Peck seem identical with the Minnesota types and also with *G. polychrous*.

NEW YORK BOTANICAL GARDEN.

THE METHOD OF CLEAVAGE IN THE SPORANGIA OF CERTAIN FUNGI

CARL A. SCHWARZ

[WITH PLATES 15 AND 16 AND TEXT-FIGURES A-F]

The division of the multinucleated sporangia into spores and the delimitation of the sporangium from the sporangiophore by a dome-shaped cross partition present many features of special cytological interest. Erroneous views on both processes are still current in the literature and as to the formation of the columella certain textbooks, both old and recent, are still entirely out of harmony with the facts. The literature dealing with the common molds, *Mucor* and *Rhizopus*, constitutes some of the earliest contributions to mycological research.

Corda (11), the "father of microscopic mycology," gave us the first description and illustration of the method of the columella and spore formation in *Ascothoria mucedo*, now known as *Rhizopus nigricans*. He writes: "Nun rundet sich die kolbige Verdickung allmählig, und gleichzeitig erfüllt die gelbe Masse ihren Hohlenraum völlig . . . aus dem unteren Theile mit dem Stiele verbunden beginnt allmählig die polsterartige Erhebung der Columella, und gleichzeitig beginnt die obere Masse undeutliche und noch isolirte Zellen zu bilden welche sich vermehren und endlich in enger Verbindung die ganze Sporangie erfüllen." His figure 78 (5-9) depicts the columella as at first slightly arched and gradually pushing up into the sporangium, while the spores are represented, at their very inception, as polyhedral masses. These figures of Corda are doubtless responsible for the persistent, erroneous accounts of the columella formation still to be found in certain textbooks, though Corda's statements were soon contradicted by Fresenius.

Fresenius (20), also studying *Rhizopus nigricans*, states he was unable to observe the phenomena described and figured by Corda. He writes: "Was über Bau und Entwicklung der Sporen bei Corda gesagt und abgebildet ist scheint mir völlig aus der Luft gegriffen zu sein." Further, also as early as 1872, Brefeld (7),

studying *Mucor mucedo*, made the following statement: "Die Scheidewand ist nicht etwa ursprünglich horizontal und erhält ihre gewölbte Form durch Dehnung unter dem einfluss des Druckes der Flüssigkeitssäule im Fruchträger, wie mehrfach angegeben wird, sie hat in der ersten Anlage die gewölbte Gestalt, die nachträglich nur unwesentlich modificirt wird."

Mucor mucedo and *Rhizopus* have been used as types not only in advanced and elementary textbooks of botany, but in many so-called textbooks of biology. Here especially the desire to elaborate in detail on the life processes beyond what is in the literature has led to many false statements, which should certainly be corrected in the interest of sound teaching. Illustrations of such incorrect statements are found in the following texts:

Bessey (4) figures and describes the development of the sporangium of *Mucor mucedo* as follows: ". . . the vertical hyphae which are filled with protoplasm become enlarged at the top and in each a transverse partition forms (I, a, fig. 159), the portion above the partition (b, fig. 159) becomes larger, and at the same time the transverse partition arches up (B, a, fig. 159), finally appearing like an extension of the hypha, and is then called the columella (C, a, fig. 159)." Reynolds Green (21), referring to *Mucor mucedo*, states: "A septum is formed close to the apex of the hypha, cutting off a small head, which grows and becomes globular. The lower cell grows also and projects into the swollen portion, forming a columella." Parker (40), referring to *Mucor*, states: ". . . The sporangium continues to grow, and as it does so the septum becomes more and more convex upwards, finally taking the form of a short club-shaped projection, the columella, extending into the interior of the sporangium." Atkinson (1) writes: ". . . at the same time that this end cell is enlarging the cross wall is arching up into the interior. This forms the columella." Coulter, Barnes and Cowles (13), referring to the Mucorales, write: "After the terminal sporangium cell is cut off, the separating wall bulges into the sporangium cavity, forming the so-called columella." Bigelow (5) incorporates in his text Parker's faulty figure of the method of the columella formation. Nathansohn (38) states: ". . . durch eine Querwand schnürt sich an deren Spitze eine

Zelle ab, schwillt zur Kugel an, in deren Hohlraum sich die Querwand meist mehr oder weniger einstülpt und die sog. Columella bildet." In so recent a textbook as Densmore's *General Botany* (17) we find: "This sporangial cell now expands with great rapidity and with its expansion the wall separating it from its hyphal stalk grows in surface area and assumes a convex form, protruding into the growing sporangium until it comes to occupy fully one half or two thirds of the sporangial cavity, when it is called the columella." Densmore also figures (fig. 141) the columella as at first a plane wall, which is later arched up into the sporangium.

The method of spore formation in sporangia was studied, with interesting results, as early as 1859, following the discovery of cell formation by division, as worked out by Von Mohl and others, and has been prosecuted up to the present day. While the pioneers were influenced and sometimes misled by theories relative to cell formation in general, the fact remains that as early as 1859 Pringsheim (44) observed and figured progressive cleavage from the surface inward, essentially as we know the process today, in the sporangia of *Lagenidium entophyllum* (Pringsheim), Zopf (*Pythium entophyllum* Pringsheim). He writes as follows: "Erst vor der Oeffnung des Sporangium beginnt nun in dem ausgetretenen, zur Kugel zusammen gehalten Inhalt, eine an der Peripherie beginnende und nach dem Centrum vorschreitende Sonderung durch welche die Protoplastmakugel schliesslich in eine grössere Anzahl von Schwarmsporen zerfällt [Pl. 8, fig. 1b]."

General conclusions relative to spore formation in sporangia found in some recent papers are quite at variance with observations which seem well established by earlier students. One must infer that some of the recent writers must have overlooked Rothert's (46) paper entitled, "Die Entwicklung der Sporangien bei den Saprolegnien."

The general history of this literature has been treated by Swingle (50) and recently by Moreau (37) and Harper (25). I shall refer only to points bearing on matters that seem still unsettled, especially the question as to the occurrence of so-called simultaneous cell-division.

Van Tieghem (55-56-57), in a series of papers dealing practically with the entire group of Zygomycetes, undoubtedly laid the foundation for the later conception of simultaneous division. In reference to *Sporodinia*, he writes as follows: "Le protoplasma sporigène se sépare d'abord en deux substances très différentes. La première toujours granuleuse, se condense en petites portions polyédriques qui deviendront bientôt autant de spores."

Twenty years later Leger (34), in his very fully illustrated thesis, dealing with fourteen species of Zygomycetes, quotes Van Tieghem's reference to the manner of spore formation in *Sporodinia* and adds: "En somme, ce passage montre d'une façon très exacte le développement des spores dans ses traits principaux." The discovery of cell-plates in the division of the cells of the higher plants undoubtedly influenced the conclusions of many students of spore formation.

Strasburger (48-49) for *Saprolegnia* and *Mucor mucedo*, Büsngen (8) for the Saprolegniales, *Phytophthora*, *Cystopus* and *Mucor mucedo*, Ward (59) for *Phytophthora infestans*, and Maurizio for *Olpidiopsis* state that the cell-division in these forms is by cell-plates.

Fischer (19), studying spore formation in the sporangia of *Woronina*, describes the process as follows: "der Zerfall des Sporangiumplasma in eine der grosse desselben entsprechende Anzahl anfangs polyedrischen Portionen, die zukünftigen Schwärme." Van Tieghem, as noted, refers to a condensation into polyhedral portions. Fischer observes a breaking up into polyhedral masses. It is interesting to note that the same author (Fischer (19)) regarded the spore plasm of *Olpidiopsis* and *Rozella* as suddenly forming rounded spores. In the former case he writes: "Mit einem male zerfällt das gesammte Inhalt in scharf umschriebene rundliche Theilchen. . . ." In the latter case he states: "Plötzlich zerfällt nun in einem gegebenen momente das Protoplasma in eine menge rund umschriebenen Portionen die zukünftigen Zoosporen." Pringsheim (43-45) regards the spore formation as occurring "unmittelbar" (directly) in *Achlya prolifera*, *Olpidiopsis*, *Rozella*, and *Woronina*.

Strasburger (48) was perhaps the first to use the term, simul-

taneous, as describing spore formation: "In den Zoosporangien der Saprolegnien wird, wie aus zahlreichen Angaben bekannt, eine grosse Anzahl Schwarmsporen simultan aus dem gesamten Protoplasmatischen Inhalte des Sporangium gebildet."

Dangeard (14), studying spore formation in *Synchytrium taraxaci*, calls it simultaneous fragmentation. Popta (42), who was concerned with the question of periplasm and spore formation in the so-called *Hemiasci*, refers to spore production in *Protomyces bellides* as "Simultan und sehr rasch." Barrett (3), investigating some species of *Olpidiopsis*, states that segmentation of the sporangial contents is apparently simultaneous throughout.

Cornu (12), studying the Chytridiales, parasitic on Saprolegniales, refers to spore formation in *Olpidiopsis* as follows: "Presque sans transition, le contenu s'organise en petites masses spheriques, futures zoospores." He claims that a similar phenomenon occurs in the sporangia of *Rozella* and *Woronina*. Thus in the above-mentioned genera the spore plasm is said to organize, with practically no transitional stages, into spherical masses.

Büsgen, who, as already mentioned, made a comparative study of a number of Saprolegniales, Peronosporales, and Mucorales, combines the conceptions of cell-plates and division, not always simultaneous. He says: "Unter auftreten von Zellplatten theilt sich der gesammte Inhalt des Sporangiums—nicht immer simultan—in etwa gleich grosse, meist nicht regelmässig begrenzte Portionen. . . ."

Rothert (46), in a quite thorough piece of work on *Saprolegnia*, figured clefts from the central vacuole proceeding outward. Humphrey (29), studying the Saprolegniales of America, merely states his agreement with Rothert as to cleavage and spore formation.

Thaxter (51) finds spore formation simultaneous in *Syncephalastrum*, but occurring by progressive constriction in *Syncephalis pycnosperma*, *S. nodosa*, *S. Wynnace*, *S. cordata*, and in a *Syncephalis* closely allied to the latter.

Kusano (32) and Griggs (23) hold that spore formation in *Synchytrium puerariae* and *Rhodochytrium*, respectively, may be either simultaneous or progressive. Davis (15), studying spore formation in the sporangia of *Saprolegnia*, Wager (58) in *Poly-*

phagus Euglenae, and Butler (9) in *Pseudolpidium aphanomycis* record spore formation as proceeding from the center to the periphery by cleavage, but do not refer to it as progressive. Likewise, Hartog (27), investigating *Pseudospora Lindstedii*, a monadine parasitic on *Saprolegnia*, figures cleavage by vacuoles extending to the periphery of the protoplasmic mass, but does not refer to it as progressive. Davis (16) figures progressive cleavage in the sporangia of the alga, *Derbesia*, by means of furrows starting from the periphery and proceeding inward. Loewenthal (35) has studied spore formation in *Olpidium dicksonii* and *Zygorhizidium willei* and Griggs (22) has studied *Monochytrium*, but both authors leave the question unsettled whether the cleavage is progressive or simultaneous.

In 1899, Harper (24), studying cell-division in sporangia and asci, pointed out that in the sporangia of *Synchytrium decipiens* the cleavage is accomplished by furrows, which form on the surface of the initial cell, and by growing deeper in a more or less radial fashion divide the protoplasmic mass, successively, into smaller portions. Harper also investigated the spore and columella formation in *Pilobolus crystallinus* and *Sporodinia grandis*. He finds, as Brefeld had stated, that the columella is not first a plane wall, which is eventually pushed up into the sporangium, but that it is from the first dome-shaped, a layer of vacuoles appears near the inner boundary of the dense spore plasma, which subsequently flatten and fuse and thus delimit the spore plasma from the columella plasma. In the case of *Pilobolus* the columella formation is aided by cleavage furrows cutting in at the base of the sporangium.

In *Pilobolus*, as in *Synchytrium decipiens*, the cleavage is progressive and is initiated by the formation of surface furrows which deepen and finally cut the plasma into protospores. In *Synchytrium decipiens* the uninucleated protospores become multinucleated and enlarge to form the spores which in germination again become sporangia. In *Pilobolus* the progressive cleavage leads to the formation of one or few nucleated protospores. These protospores become multinucleated, increase in size, and divide until finally oblong, binucleate sporangiospores are produced. In *Sporodinia*, Harper finds an abbreviated process of spore formation in that the

progressive cleavage, by surface furrows and clefts, divides the spore plasm into multinucleated, polygonal blocks of very variable size which round up at once and become the definitive spores.

Swingle (50) finds cleavage in the sporangia of *Rhizopus nigricans* much like that in *Sporodinia*, except that the spores are more uniform in size and have thicker walls. In *Phycomyces* the spore plasm is divided by vacuoles, which become angular and fuse to form irregular clefts. Spore formation is aided by furrows which cut into the spore plasm from the columella cleft. Swingle agrees with Harper as to the method of columella formation.

Timberlake (52) describes spore formation in the sporangia of the alga, *Hydrodictyon*, as a progressive cleavage by means of furrows. Percival (41) and Rytz (47), discussing spore formation in *Synchytrium endobioticum* and *Synchytrium succissae*, respectively, both agree that spore formation is brought about by progressive cleavage.

In 1913, Moreau (37) described the spore formation in a number of Zygomycetes. His study may be summarized as follows:

In *Circinella conica* spore formation proceeds by means of vacuoles, which separate fragments of protoplasm having the form of amoebae. The protoplasm contracts around each nucleus, rarely around two nuclei, forming protospores which he compares to those described by Harper for *Pilobolus*. The nuclei then divide and lead to the formation of multinucleated spores. Moreau states that for *Phycomyces nitens* and *Rhizopus nigricans* his observations agree in general with those of Swingle, but on page 32 he refers to the protoplasmic segments as being "amiboide" and connected by trabeculae. In *Mucor spinescens*, Moreau finds that a confluence of vacuoles leads to the formation of elongated protoplasmic threads. The threads become nodose, each nodosity containing one or two nuclei and finally forming a spore. Moreau states that a similar thread stage may be observed in the spore formation in *Absidia glauca* and *Absidia septata*. In *Syncephalastrum cinereum* and *Syncephalastrum racemosum* the spores are said to be formed by a condensation of protoplasm into spherical or elliptical masses, each enclosing one or more spores; generally there is but one nucleus in each spore. Moreau's description of

spore formation, in the above-mentioned zygomycetes, is extremely fragmentary and certain of his figures suggest that his material was poorly fixed.

METHODS

The *Saprolegnias* were grown on small flies of the genus *Drosophila*. They were frequently parasitized by *Olpidiopsis* and *Rozella*. Cultures on the flies were then transferred to slightly cooled agar plates. A drop of water was then placed on each fly so that the sporangiferous filaments might float out into their normal position. Slightly cooled agar was then gently dropped over each fly. The cultures were then exposed out-of-doors to quickly congeal the agar. The halo of filaments was still easily discernible. Blocks of agar containing the entire host were now cut out and transferred to weak Flemming and Merkel fixatives. The washing, dehydrating, and imbedding was done as usual. The sections were cut 5 μ thick, stained with the Flemming triple combination, cleared very quickly in clove oil, and mounted in Canada balsam.

Cleavage in *Saprolegnia* was also studied in hanging-drop cultures, and *Olpidiopsis* was also studied in the same manner. The Zygomycetes were cultured upon sterilized bread in jelly glasses. In order to retain the loose, open structure of the bread, which facilitates the growth of the mycelia, only a small amount of water was poured into each jelly glass before sterilization. When the sporangia assumed a snow-white appearance, under the hand-lens, wefts of the fungus were cut out with sharp-pointed scissors and immediately transferred to the fixatives. The conglomerated mass of hyphae was then gently pushed down into the fixative and the vial was shaken to dislodge the air-bubbles. The material was fixed for 24-48 hours in Merkel's solution, or for one hour in one part of weak Flemming and two parts of water, and then transferred to Merkel's fixative. By these means blackening of the fungus was prevented and bleaching with hydrogen peroxide was unnecessary.

The fixative was now poured off and the vial was carefully filled with water and tilted into a dish of water. The fungus was repeatedly floated into a vial and transferred into fresh water. The material, thus washed for two to two and one half hours, was

then dehydrated, beginning with 15% alcohol, and imbedded in paraffin. The sections were cut 5μ thick, stained by Flemming's triple method, cleared quickly in clove oil, and mounted as usual.

OLPIDIOSIS

Pringsheim (45) gave us the first account of spore formation in the sporangia of *Olpidiopsis*, a parasite, which he mistook for the antheridia of *Saprolegnia*. He speaks of the spores as "Samenkörper" and says that they are formed directly (unmittelbar), and that similar phenomena may be observed in the structures which we now recognize as the sporangia of *Rozella* and *Woronina*.

In 1872, Cornu (12) published a paper in which he supported A. Braun (6) in reference to the parasitic nature of *Olpidiopsis*. He noted the appearance of large centrally disposed vacuoles, their disappearance, and the formation of a foamy protoplasm. Both Cornu (12) and Fisher (19) agree that the spores are formed directly.

Maurizio (36) states that cell-plates are formed in spore formation in *Olpidiopsis major*. As already mentioned, Loewenthal is not clear as to whether spore formation in *Olpidium dicksonii* and *Zygorhizidium willii* is simultaneous or by progressive cleavage.

In Butler's (9) account of spore formation in *Pseudolpidium aphanomyces* he states that the spore "Anlage" originate as a result of "heapings of protoplasm," which are few in number as compared with the number of zoöspores produced. Butler compares this stage with that Harper describes in *Synchytrium*, where the early stages of cleavage give rise to multinucleated masses of protoplasm. Cleavage fissures then extend from the vacuole to the sporangial wall, the vacuolar and protoplasmic membranes then rupture, and the "Anlage" swell and fuse. The sporangium is now filled with a homogeneous mass. Butler states: "Five or ten minutes later final fashioning of the zoöspores is complete and movement commences in the sporangium." Butler records cleavage furrows extending from the vacuole to the sporangium wall, but he does not figure them. His figure 6C, plate 9, which he interprets as a "condensation of protoplasm into heaped masses,"

appears to be a stage prior to the enlargement and fusion of the vacuoles into a large central vacuole.

Barrett (3) studied both living and stained material of a number of *Olpidiopsis* species. He reports that he could not detect any signs of the protoplasmic heapings described by Butler within the sporangium. If one studies the figures in plate 24, one is led to believe that Barrett did not find the crucial stages of spore formation. This leads him to the erroneous conclusion that "fragmentation of the protoplasm is simultaneous."

Kusano (33) investigated the life history and cytology of *Olpidium viciac*. He was unable to find evidence of progressive division, but states "that a clear space appeared in the cytoplasm all at once between each two nuclei, and that the protoplasm was cut up into as many polygonal parts as there were nuclei." It seems obvious that this statement refers to the stage following what Strasburger and Büsgen regarded as a stage of coalescence of the spore origins which is not real, but only apparent.

The stages in the life history of *Olpidiopsis saprolegniae*, prior to the formation of spores, have been discussed and figured by a number of authors. From a study of the living material, in hanging-drop cultures, I am able to confirm the existence of large centrally disposed vacuoles in young sporangia, the increment in size, and subsequent coalescence of these vacuoles. The process of spore formation, as I have observed it, is entirely at variance with that described by the above-mentioned authors. The phenomena I observed were very similar to processes of spore formation in the sporangia of *Saprolegnia* and *Achlya* as I have found them and not as described by Strasburger, Büsgen, and Haftog. I was able to note the following changes by observing living specimens in hanging-drop cultures. The history of one sporangium is as follows:

At 7:40 P.M. the sporangium had a large central vacuole, and in the median plane a blunt cleavage furrow could be seen extending toward the periphery (text fig. A, 4). Three minutes later the vacuole became irregular and one sharp and two blunt cleavage furrows were visible (text fig. A, 5). Four minutes later the vacuole had increased in size so that the protoplasm formed a rather thin peripheral layer. Sharp cleavage furrows were now

evident (text fig. A, 6, 7), and after the elapse of one minute they cut through the latter and the large vacuole disappeared. Cleavage is now complete and here and there the outlines of the spores can be made out (text fig. A, 8). After two minutes the protoplasm became very granular and the hazy outlines of polygonal spore masses were recognizable. I can only interpret this polygonal stage as due to rapid growth of the spore initials, which thus press against one another and become polyhedral. One minute after the appearance of the compact, polygonal spore initials a contraction occurred, the inter-spore substance appearing as hyaline lines.

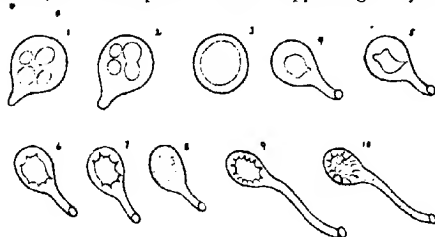


Fig. A. *Olpidopsis saprolegniae*: 1-2, median view of sporangia showing several rounded vacuoles; 3, sporangium showing coalescence of the vacuoles; 4-8, different series than 1-3 in which the wall layer is thinner; 4-5, sporangia showing vacuoles of various shapes; 6-7, sporangia showing early cleavage stages; 8, sporangium showing apparent homogeneous stage following the rupture of the plasma membrane; 9-10, another individual, sporangia show radial furrows; 10, cleavage has occurred in the exit tube. 1-2 and 4-10 show exit tubes.

One minute later the spores underwent a further contraction; they rounded up and almost immediately began to move to and fro. Within two minutes the zoospores escaped through the exit tube. Thus within eighteen minutes of the first formation of a cleavage furrow the spores formed and escaped. If one considers the rapidity of these changes, one can readily infer why the cleavage furrows, extending outward from a central vacuole, are so seldom seen in fixed sections. I can not agree, therefore, with Barrett that the spore formation occurs simultaneously. I would interpret his figure 30 as a contraction stage following the so-called homogeneous state, of Strasburger and Büsgen, in which the spore initials are so closely pressed together that their boundaries are

almost obliterated. Nor can I agree with Butler, who describes the formation of "protoplasmic heapings" and the delimitation of multinucleated, protoplasmic masses, which are later cut up by cleavage furrows, to form the spore origins. In no case did I observe any fusion of spore initials and the resulting production of a homogeneous state such as Butler describes for *Pseudolpidium aphanomyces* and as was held by Strasburger and Büsgen to occur in *Saprolegnia*.

We can summarize, roughly, the following stages in the spore formation of *Olpidopsis saprolegniae* Cornu:

1. Protoplasm with many small vacuoles.
2. The formation of large vacuoles more or less centrally disposed and the concomitant production of an exit-tube.
3. The coalescence of large vacuoles into a large central vacuole.
4. Progressive cleavage by furrows cutting outward from the central vacuole. (First contraction phase.)
5. Cleavage of plasma membrane, shrinkage of the sporangium and disappearance of the central vacuole.
6. Swelling of the spore initials to the polygonal closely pressed areas commonly observed.
7. Second contraction phase—appearance of hyaline spaces between spore initials (often erroneously interpreted as cell plates).
8. Further contraction leading to the rounding up of the spore masses and their swarming movements.

The above conclusions were reached after carefully studying the cleavage phenomena in dozens of sporangia in hanging-drop cultures.

SAPROLEGNIA AND ACHLYA

Rothert (46) recognized three types of sporangia in the Saprolegniaceae: "gefüllte Sporangien," those completely filled with protoplasm; "inhaltsarme," those having a thin parietal layer of protoplasm; and "normale," sporangia with a thick parietal layer, the predominant form. Rothert figured furrows cutting through the protoplasm from the central vacuole outward and notes that these furrows appear practically simultaneously throughout the whole length of the sporangium. Rothert's observations on spore formation in *Saprolegnia* and *Achlya* are of great importance for understanding the cleavage phenomena in the other sporangia. Harper has reviewed and confirmed Rothert's observations in sev-

eral points, but recent students have in a number of cases failed to take account of the evidence he has presented as to the contraction and expansion phases accompanying cleavage. I have studied *Achlya* and *Saprolegnia* in both living, sectioned, and stained material, and my observations confirm those of Rothert.

The process of cleavage is similar to that I have already described for *Olpidiopsis saprolegniae*. The cleavage is progressive, the furrows appear first on the inner surface of the parietal protoplasmic layer and give the latter an undulated appearance. Gradually these clefts become sharper and reach the plasma membrane. In optical view these protoplasmic masses resemble the old-fashioned sugar-loaves. Viewed from the surface the protoplasmic masses are roughly polygonal. The spore initials are generally described as being connected by fine protoplasmic strands. I am inclined to interpret these strands as gelatinous exudates of the spore initials. Rothert described the development of spores in very slender sporangia as a heaping of protoplasm on the protoplasmic membrane. It is a question whether there is much, if any, increase in the radial diameter of the protoplasmic layer on the median axis of the spore initials. A better interpretation of the spore formation in these sporangia and in the oogonia is to regard it as a process of cleavage, the furrows being at first broad and shallow instead of sharp and deep.

The spore initials now contract and the clefts become prominent. The protoplasmic masses now become densely granular, are highly refractive, and assume more definite outlines. This stage is quickly followed by a splitting of the protoplasmic membrane which is drawn in by the isolated spore initials as they round up. Division of the protoplasmic content is now complete, each definitive spore is uninucleated and is homologous with the uninucleated protospores Harper described in *Synchytrium decipiens*.

As first noted by Rothert and confirmed by Harper, the splitting of the elastically stretched plasma membrane is attended with a marked shrinkage of the sporangium wall accompanied by the expulsion of part of the cell-sap through the sporangial wall. The basal septum, which has heretofore been concave, is now pushed up by turgor into the sporangium and assumes a convex configura-

tion. Rothert estimated the shrinkage at 13 per cent. Butler (9) finds that at a corresponding stage the diameter of the sporangium of *Pythium intermedium* decreased by about one tenth. The same author also noted a contraction of the sporangium of *Pseudolpidium aphanomycis* immediately after the disappearance of the large central vacuole. Harper called attention to the fact that in *Synchytrium decipiens* the cleavage was accompanied by pronounced shrinkage. He found that when cleavage was complete the total volume of the segments had been reduced to such an extent as not to occupy more than approximately one third of the volume of the primordial cell. Kusano also reports a shrinkage of the segments in the sporangia of *Synchytrium puerariae* during the cleavage process.

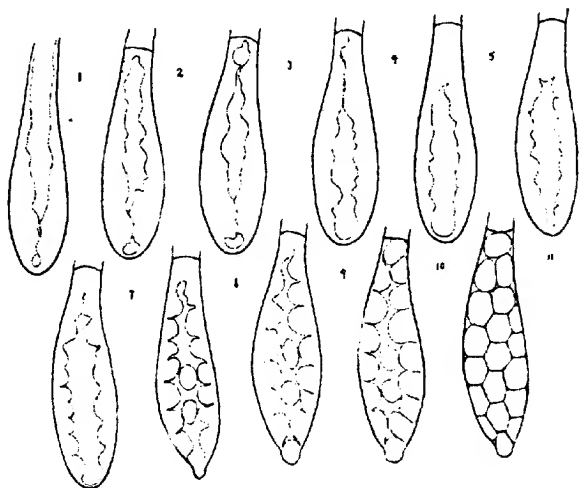


Fig. 8. *Saprolegnia torulosa*: 1, tip of hypha which will become a sporangium; 2-7, show varying appearances of the central vacuole; 7, first appearance of cleavage, furrows irregular and not corresponding to the definitive furrows; 8-9, spore masses outlined by rather shallow furrows, the two oval outlines in these figures, and also in figures 10, represent the end views of spore initials projecting up from below; 10, clefts have become deeper; 11, spores have become polygonal through mutual pressure; this stage soon follows the rupture of the plasma membrane and represents an expansion phase of the spores; the basal wall is now convex toward the sporangium showing that its plasma membrane is ruptured.

Text figure B, 1-11, represents the lengths and breadths of a sporangium at successive stages in spore formation. The micrometer measurements are as follows:

9:12 P.M.	86 μ long—26 μ wide
9:27 P.M.	88 μ long—26 μ wide
9:37 P.M.	90 μ long—25 μ wide
9:56 P.M.	92 μ long—25 μ wide
10:05 P.M.	93 μ long—25 μ wide
10:10 P.M.	94 μ long—28 μ wide
10:17 P.M.	90 μ long—27 μ wide
10:22 P.M.	92 μ long—26 μ wide
10:30 P.M.	86 μ long—22 μ wide
10:34 P.M.	Spores moved to and fro.

At 10:10 P.M. the sporangium had reached its maximum size; the basal wall was concave, due to the turgor within the sporangium. At 10:17 P.M. the clefts apparently cut through the plasma membrane, the spore initials rounded up, and the sporangium decreased four microns in length and one micron in diameter. The basal wall was now flattened. This stage of contraction was followed by the expansion stage. The spore initials became tightly pressed together, the protoplasm assumed a homogeneous appearance, and the spore outlines were only visible as very faint lines. This is the stage that deceived Strasburger (48), for he writes as follows: "Wiederholt sind mir Fälle vorgekommen in welchen nach dem die Sporenanlage es schon bis zur Bildung der Körnergrenzen ja selbst Hautschichtgrenzen gebracht hatte, plötzlich die ganze Entwicklung rückgängig wurde, alle Trennungsandeutungen schwanden und das Sporangium alsbald wieder von gleichmässig kammerigen Protoplasma gefüllt erschien. Dann nach kurzer Zeit, wurde die Entwicklung, und zwar nun auffallend schnell wieder aufgenommen. Eine solche zweite fiel mir, im Verhältniss zu der Ersten stets durch die grosse Regelmässigkeit der Theilstücke auf."

The great expansion following the delimitation of the spore initials, the temporary loss of the granular character of the spore protoplasm, the obscuring of the cell boundaries through close contact, and the subsequent contraction which reveals the polygonal spore masses have given rise to much confusion. Butler (9), in 1907, speaking of spore formation in *Pythium proliferum*, writes: "From this I have been led to suppose that even at this stage the

spore origins are definitely formed, and that, though fused into a mass in which individual spores can not be made out, yet each nucleus has obtained a hold on a certain mass of cytoplasm. . . ."

The sudden appearance of the polygonal spore masses at the beginning of the second contraction phase has given rise to such theories as the simultaneous cleavage of the sporangial protoplasm into polygonal masses and the cutting out of the spores by cell-plates. I have already summarized these views and I need not repeat them here.

The polygonal spores of *Saprolegnia* undergo a further contraction and subsequently round up. The turgor in the sporangium is decreased to such an extent that the basal wall now becomes convex inward. At this stage the sporangium decreased still more in length. Thus during the period of greatest turgidity the sporangium measured 94 microns in length. When the spores were fully matured the sporangium had contracted eight microns in length and six microns in width.

The observations of Rothert (46) relative to the escape of the cell-sap and the concomitant shrinking of the sporangium during spore formation in *Saprolegnia*, Harper's evidence of similar phenomena in *Synchytrium decipiens*, Kusano's observation of shrinkage in *Synchytrium puerariae*, Swingle's account of progressive cleavage in *Rhizopus nigricans* and *Phycomyces nitens*, Harper's studies of spore formation in the sporangia of *Sporodinia grandis* and *Pilobolus*, Butler's observations relative to shrinkage in the sporangia of *Pythium intermedium* and *Pseudopodium aphanomyces*, Harper's and Dodge's observations of the extrusion of water into vacuoles during the early stages of the formation of sporangia in *Trichia*, as well as my own observations, lead me to corroborate the contention of Harper that the exudation of water is a factor in the process of segmentation of the protoplasm. Harper compares the furrowing of the spore plasm with the cracking of a drying, colloidal mass. The fact that vacuoles or furrows never cut out protoplasmic segments devoid of nuclei is proof that the latter are the centers which control the water loss and thus the cleavage process. This may be explained by assuming that the nucleic acids manifest an attraction or affinity for water greater

than that displayed by the cytoplasm; hence, as Harper has suggested, the loss of water may be least in the vicinity of the nuclei.

SPORODINIA GRANDIS

Spore formation in the sporangia of *Sporodinia grandis* was regarded by both Van Tieghem (55) and Leger (34) as a condensation of the spore plasm into polyhedric masses, which later round up. Harper (24) has figured a number of stages in spore and columella formation. Swingle (50), a few years later, studied the same fungus and reports that his results are entirely in accord with those of Harper.

As *Sporodinia* represents an extreme type as to the speed of spore formation, I have studied the process further in the light of the conceptions of contraction and expansion first developed by Rothert from his studies on the sporangia of *Saprolegnia*. I find the dome formed by series of large vacuoles, which flatten, fuse, end to end, and separate the spore plasm from the columella plasm as described by Harper. I have, however, a number of slides (Pl. 15, figs. 1, 6) which show an interesting variation of the process in that the vacuoles are completely fused on one side of the sporangium, while on the other side they are either somewhat globose or flattened. Swingle's fig. 8, plate 2, shows that in *Rhizopus nigricans* the columella formation may be more advanced on one side of the sporangium. A few times I observed surface furrows cutting in at the base of the sporangium, to meet the flattened vacuoles, which cut out the columella (Pl. 15, fig. 6). Harper has described a similar phenomenon in *Pilobolus* and Swingle in *Rhizopus nigricans*.

In *Sporodinia* spore formation may begin before the columella cleft is complete. Swingle notes that this often occurs in *Rhizopus nigricans* (see his fig. 8, plate 2). This shows, it seems to me, that the columella formation and cleavage are two parts of one general contraction phase. The cleavage is progressive and may begin by the formation of furrows at the surface or at the columella cleft (Pl. 15, figs. 1, 2). It is to be noted that cleavage is more advanced in that region where the fusion of vacuoles has produced the columella cleft (Pl. 15, fig. 6). The furrows cut

inwardly and as the spore plasm is giving off water the clefts widen. The furrows from the surface appear to cut into the spore plasm in a centripetal fashion. They meet and fuse with those furrows which started from the columella cleft and cleavage is thus completed; the protoplasm has been cut up into a mass of irregular blocks which are variable in size and are multinucleate. These spore initials represent, as compared with swarm spores of *Saprolegnia* and the protospores of *Synchytrium decipiens*, *Pilobolus crystallinus*, *Circinella conica*, etc., a premature completion of spore formation. They correspond to the multinucleate masses preceding the protospores. As in *Rhizopus nigricans*, the spores of *Sporodinia grandis* are multinucleate at their inception. When cleavage is complete the spore initials present a dense granular appearance. The protoplasmic mass is also somewhat shrunken. Soon, however, the spore initials take up water and grow, the protoplasm becomes less granular and takes on a lighter stain. The spores become so tightly pressed together that their protoplasmic membranes assume polyhedral outlines, which are so thin that they are traced with difficulty under the oil-immersion objective (Pl. 15, fig. 4). This stage is homologous with the so-called homogeneous stage, which Strasburger and Büsgen described for *Saprolegnia*. This period of growth is followed by a second contraction. The spores now develop a thin wall, contract slightly, and round up.

I have illustrated the chief stages of the development of the columella and spores in *Sporodinia grandis* in a series of text figures (text fig. C, 1-5).

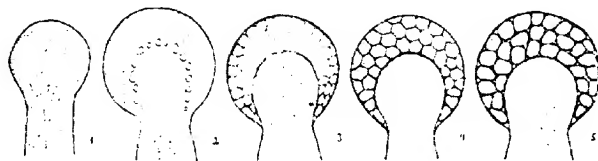


Fig. C. Diagrams showing the method of the columella and spore formation in *Sporodinia grandis*, the nuclei appearing as mere dots. 1, a young sporangium. 2, showing the dome-shaped layer of vacuoles outlining the columella. 3, showing early stage of progressive cleavage. 4, showing the polyhedral stage. 5, mature spores.

MUCOR RACEMOSUS

Apparently no one since Leger (34) has studied spore formation in *Mucor racemosus*. Leger claims for it, as for all sporangia, that the spores are cut out simultaneously as polyhedral blocks.

Moreau (37) has studied *Mucor spinescens* and he describes vacuolization of the protoplasm resulting in long strands, which become nodular and then break up into uninucleate or several, nucleated spores. He gives no further account of the process.

I have studied *Mucor racemosus* relative to the process of spore formation. I find that spore formation is initiated by furrows, which start at the periphery of the spore plasma and cut out multinucleated blocks of irregular size (Pl. 16, fig. 16). Further furrowing cuts up these blocks into irregular protoplasmic masses containing a few nuclei. These protoplasmic masses then grow and become polyhedral. This expansion stage is followed by a second contraction, the spores round up and develop a cell-wall. The mature spores may contain seven to eight nuclei. I have not observed a protospore stage. The process of spore formation, as in *Sporodinia grandis*, is abbreviated, but the spores have thicker walls and are viable for a longer period. They are also more uniform in size than those of *Sporodinia grandis*.

CIRCINELLA MINOR

Moreau (37), studying spore formation in *Circinella conica*, states that the center of the sporangium is at times occupied by a large vacuole. The formation of spores is accomplished by irregular vacuoles, which cut up the spore plasma into amoeba-like bodies bound together by protoplasmic strands. These strands become thinner and break, the protoplasm then contracts about each nucleus, rarely around two. Moreau compares these protoplasmic bodies to the protospores Harper described in *Pilobolus crystallinus*. The nucleus then divides and each protoplasmic mass becomes multinucleated, the spores become polygonal and press against one another. At maturity they become globular and smooth.

I have studied spore formation in *Circinella minor*, but my observations do not agree entirely with those of Moreau. Cleavage,

as I have observed it, is similar to that Harper described in *Pilobolus*. Furrows appear at the surface of the spore plasm and cut inwardly to meet the clefts produced in the interior of the spore plasm by vacuoles, which become angular (Pl. 16, fig. 8). The spore plasm is thus cut up into irregular protoplasmic blocks containing a variable number of very small nuclei (Pl. 16, fig. 8). Moreau does not describe or figure cleavage furrows in *Circinella canica*. The irregular blocks are further divided by cleavage into more or less oblong to sausage-shaped protoplasmic masses containing four to five nuclei (Pl. 16, fig. 9). As in *Pilobolus*, these blocks are transversely divided into roughly polygonal, one- to two-nucleated protoplasmic masses. I agree with Moreau in calling these protoplasmic segments the protospores. During the cleavage process the protoplasmic mass undergoes shrinkage without question, but I did not observe such a loose and open structure of the dividing spore plasm as Moreau figures, and I am inclined to believe that his figure 28, plate 3, represents poor fixation and considerable shrinkage. The protospores are, for a time, connected by delicate, gelatinous strands, which are probably an exudate of the protoplasm (Pl. 16, fig. 10). The nuclei now divide and each protoplasmic mass (protospore) swells and grows. The young spores now become polyhedral and are closely pressed together (Pl. 16, fig. 13). This expansion period is followed by a contraction; the multinucleated spores round up and form a cell-wall (Pl. 16, fig. 14).

The process of spore formation in *Circinella minor* may be summarized as follows:

1. Differentiation of spore and columella plasm.
2. Formation of irregular multinucleate blocks of protoplasm by surface furrows and angular vacuoles.
3. Further division by cleavage producing oblong protoplasmic masses containing four to five nuclei (2 and 3 are contraction phases).
4. Division of oblong to sausage-shaped blocks into one- to two-nucleated protospores.
5. Protospores grow and become multinucleated (expansion phase).
6. Spores round up (second contraction phase).
7. Further contraction and formation of cell-walls.

Harper has pointed out that in *Sporodinia grandis* there is an abbreviation of the process of spore formation as compared with

Pilobolus crystallinus and *Synchytrium decipiens*. It is evident that the process of spore formation in *Circinella minor*, like *Rhizopus nigricans*, occupies an intermediate position in such a series. In *Circinella minor* the formation of protospores is followed by nuclear division and growth. But with the formation of the protospores cell-division is complete. In *Pilobolus crystallinus* the protospore grows and becomes multinucleated, but this multinucleated cell divides by constriction. The final cell-divisions produce the oblong, binucleate spores. In *Sporodinia grandis* the process of spore formation is so abbreviated that the initial cleavage cuts out comparatively large multinucleated segments which ultimately round up and become the definitive spores.

I have illustrated the chief stages of the development of the columella and spores in *Mucor mucedo* in a series of text figures (text fig. D, 1-5).

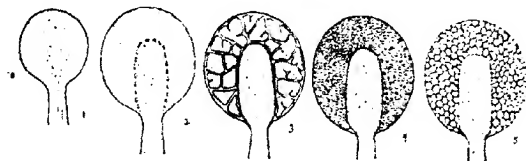


Fig. D. Diagrams showing the method of the columella and spore formation in *Mucor mucedo*. 1, a young sporangium. 2, showing the dome-shaped layer of vacuoles outlining the columella. 3, showing the spore plasma cut up into protoplasmic blocks by progressive cleavage. 4, spore-initials in the contraction stage. 5, showing the polyhedral or expansion stage.

MUCOR MUCEDO

Strasburger (49) has given us a fragmentary account of spore formation in *Mucor mucedo*. He considered the protoplasmic mass cut up by cell-plates in a manner similar to that in *Saprolegnia*. Two years later Büsgen (8), studying the same species, came to the conclusion that the spore plasma is cut up into large protoplasmic blocks by cell-plates, and that by subsequent subdivision protoplasmic masses are formed which have the size of the definitive spores. The sporangium then becomes homogeneous and a second division produces the definitive spores. Leger (34) studied spore formation in the sporangia of *Mucor mucedo* and

agrees with Van Tieghem that the spore plasm is divided at once into polyhedric granular spores separated by a non-granular substance. Moreau,¹ studying spore formation in *Mucor mucedo*, came to the conclusion that the spore plasm divides into irregular multinucleated fragments which subsequently become the spores.

I have studied the method of the columella and spore formation in *M. mucedo*. I find that the columella does not originate as a plane wall, which is subsequently arched up into the sporangium, as is so often depicted in textbooks on botany, but that as in the Zygomycetes studied by Harper (24) and Swingle (50) the columella is from the first dome-shaped as I show in Pl. 16, fig. 19; a dome-shaped series of vacuoles appear, these flatten, fuse end to end, and thus delimit the spore plasm from the columella plasm.

The spore plasm is first cut up into comparatively large protoplasmic blocks. During this stage considerable contraction occurs for the blocks are not in close apposition (Pl. 16, fig. 20). These blocks are now subdivided by cleavage into roughly polyhedral spore initials. This subdivision is attended by still further contraction, followed by an expansion stage in which the spore initials become polygonal, as figured by Leger ((34), plate 8, fig. 35; my figure, plate 16, fig. 21). These spore initials eventually contract and form the ovate definitive spores. I have not been able to determine with certainty the number of nuclei in the ripe spores.

RHIZOPUS NIGRICANS AND PILOBOLUS CRYSTALLINUS

The process of spore formation in *Sporodinia grandis* is much abbreviated, the spore plasm being cut up only into relatively large multinucleate blocks (text fig. C, 1-5), which quickly round up to form the definitive spores. In *Rhizopus nigricans* (text fig. E, 1-5) the spore plasm is cut up, progressively, into numerous much smaller multinucleate, angular to ovate spores, but never reaches the uninucleate stage. The relative extent of the cleavage is well illustrated by comparing the size of the spores of *Rhizopus nigricans* with that of those of *Sporodinia grandis*. In *Sporodinia grandis* the spores measure, on an average, 20-30 x 17-24 μ , in *Rhizopus nigricans* 9-12 x 7.5-8 μ . In *Pilobolus crystallinus* (text fig. F, 1-6) the process of spore formation is still further

¹ Bull. Soc. Mycol. Fr. 31: 71-72. 1915.

protracted. The spore plasm is cut up, by progressive cleavage, into uninucleate protospores. An embryonic stage now intervenes, the protospores grow and become multinucleate. By a series of divisions binucleate definitive spores are produced.

For the sake of comparison I have also included diagrams of *Rhizopus nigricans* and *Pilobolus crystallinus*, showing stages of the development of the columella and spores.

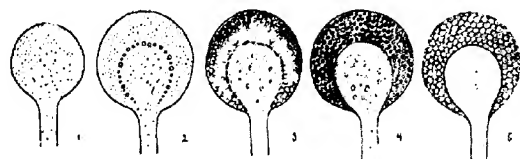


Fig. E. Diagrams showing the method of the columella and spore formation in *Rhizopus nigricans*. 1, a young sporangium. 2, showing the dome-shaped layer of vacuoles outlining the columella. 3, showing early stage of cleavage. 4, showing the contraction stage. 5, expansion or polyhedral stage.

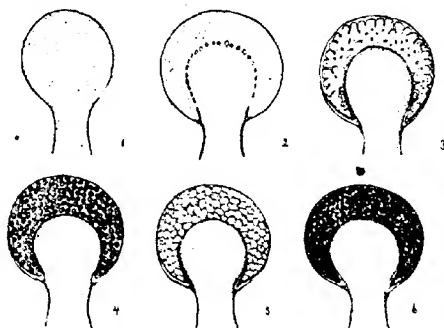


Fig. F. Diagrams showing the method of the columella and spore formation in *Pilobolus crystallinus*. 1, a young sporangium showing dense spore plasm. 2, showing the dome-shaped series of vacuoles and a circular furrow which cut out the columella. 3, stage of uninucleate protospores. 4, polyhedral stage. 5, polyhedral stage. 6, ripe spore stage.

DISCUSSION

Although a number of recent papers by Kusano (32), Barrett (3), and Griggs (23) report the occurrence of simultaneous cleavage in the sporangia of certain algae and fungi, the evidence to

prove the existence of this method of spore formation is inadequate. On the other hand, there is an accumulation of evidence which confirms the contention that cell-division in the sporangia of algae and fungi is essentially a process of furrowing either from the periphery of the sporangia or from the vacuoles in the interior of the spore plasm.

As far as I am aware Rothert, studying spore formation in the sporangia of *Achlya* and *Saprolegnia*, was the first to note the contraction and expansion phases during the cleavage process. His observations are, therefore, of paramount importance for understanding the mechanics of the cleavage phenomena in other sporangia.

A complete parallelism with the phenomena described by Rothert is found in the process of oosphere formation in *Vaucheria*, as described very carefully from living material by Oltmanns (39). Oltmanns confirms and amplifies the observations of Thuret, relative to zoöspore formation in *Vaucheria*, and Strasburger and Berthold, who studied the process of zoöspore and oogonium formation.

According to Oltmanns, just before the cell-division, which cuts off the oogonium from the parent filament, there is an extrusion of water from the protoplasmic mass within the oogonium; the extruded water forms a large vacuole at or below the base of the oogonium (figs. 8-10, pl. 6-7). This stage is comparable to the first contraction phase with its large central vacuole and the formation of radial furrows beginning the delimitation of the spores, as noted by Rothert in *Saprolegnia*. In the case of *Vaucheria*, cutting off of the oogonium is first initiated by what may be called the cleavage vacuole. The condition is similar to that found in columella formation in *Pilobolus crystallinus*, *Rhizopus nigricans*, *Phycomyces nitens*, *Sporodinia grandis*, *Mucor mucedo*, etc. Such basal vacuoles play the same rôle as the cleavage vacuoles which appear in the spore plasm of *Pilobolus*, *Phycomyces*, *Circinella*, etc.

The plasma membrane about the basal vacuole in *Vaucheria* is finally broken, the cell-sap escapes, and the oogonial protoplasm now expands; the basal plasma membrane of the oogonium and the plasma membrane of the filament are brought into close prox-

imity (fig. 9, pls. 6-7). This stage is to be compared also to the stage in the formation of the columella in sporangia of the Zygomycetes where the vacuoles flatten and fuse edge to edge. Later, in *Vaucheria*, a wall is formed between the two membranes and is seen to be convex toward the oogonium (fig. 11, pls. 6-7). The oosphere is now rounded up in the second contraction phase. The protoplasmic mass, which has heretofore conformed to the general outline of the oogonial wall, undergoes contraction until the rather globular or ovoid oosphere is formed. The ripe oosphere contains relatively few chloroplasts, but numerous oil globules, suggesting the chemical condensation processes which have accompanied the extrusion of cell-sap. Such illustrations show clearly that the process of spore formation, whether sexual or asexual, involves rather a marked series of contraction and expansion phases accompanied by metabolic changes in the protoplasm which result, in general, in the formation of reserve food products, but whose fundamental chemical nature is at present little known.

The process of spore formation may be much abbreviated as in *Sporodinia grandis*, whose spores are short lived and contain little reserve material, or it may be protracted as in *Pilobolus crystallinus* and *Synchytrium decipiens*, by the interpolation of an embryonic stage, in which the protospores increase in size, become multinucleated, ripen, form a wall, and enter a period of rest before they germinate by a tube in *Pilobolus* or by zoospore formation in *Synchytrium*.

Swingle (50) attributes spore formation in sporangia as due to localized contractions of the protoplasm. He does not believe that the nuclei directly influence contraction, but states: "The nuclei determine to some extent just what protoplasm shall constitute each individual spore."

Recently Harper (25) has suggested that the loss of water is probably least in the vicinity of the nuclei during the shrinking and condensation of the spore plasma, and that this might be a determining factor in the orientation of the cleavage furrows.

The failure to note the various contraction and expansion phases accompanying the formation of spores in the sporangia of algae and fungi has doubtless led to the erroneous conception of simul-

taneous cleavage as it still persists in the literature of spore formation.

While the method of the columella formation has been studied in relatively few Zygomycetes, the researches by Harper (24), Swingle (50), and myself have shown that the columella is not from the first a plane wall, which is subsequently pushed up into the sporangium, as is so often figured and described in textbooks on botany, but that it originates as a dome-shaped mass of vacuoles at the inner boundary of the spore plasm. Brefeld (7) observed that the columella was from the first dome-shaped. The vacuoles flatten in their radial axes, fuse edge to edge, and thus delimit the spore plasm from the columella plasm. In *Rhizopus nigricans*, *Pilobolus crystallinus*, and *Sporodinia grandis* a circular furrow cuts upward from the base of the sporangium to meet the cleft formed by the flattened vacuoles.

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EXPLANATION OF PLATES

All figures were drawn with the aid of the camera lucida, and with the Zeiss 1.8 mm. objective, N. A. 1.25; magnification about 1300 diameters.

PLATE 15

Sporodinia grandis

- Fig. 1. Median vertical section of a sporangium showing cleavage complete on one side and first appearance of superficial cleavage furrows.
Fig. 2. Median vertical section of a sporangium showing columella-cleft completely formed and furrows passing upward through the spore plasm.
Fig. 3. Tangential section of a sporangium showing an advanced stage of cleavage and a large central mucorin crystal.
Fig. 4. Oblique section of a sporangium, spores have become polygonal by mutual pressure (expansion phase).
Fig. 5. Tangential section of a sporangium representing an early stage of cleavage.
Fig. 6. Median vertical section of a sporangium, columella-cleft and cleavage complete on one side of the sporangium and in an advanced stage on the other side.

PLATE 16

- Fig. 7. *Sporodinia grandis*. Tangential section of a sporangium showing advanced stage of cleavage.

Circinella minor

- Fig. 8. Tangential section of a sporangium showing branching furrows.
Fig. 9. Horizontal section of a sporangium; spore plasm cut into oblong to sausage-shaped protoplasmic masses which are somewhat concentrically arranged and are undergoing transverse segmentation.
Fig. 10. Section of a portion of a sporangium, protoplasmic masses are being cut up into 1-2 nucleated protospores.
Fig. 11. Vertical median section of a sporangium, somewhat later stage of cleavage than shown in figure 10.
Fig. 12. Oblique section of a sporangium about same stage as the last.
Fig. 13. Spores have become multinucleated and polygonal (expansion phase).
Fig. 14. Mature multinucleated spores.

Mucor racemosus

- Fig. 15. Tangential section of a sporangium showing the beginning of two cleavage-furrows.
Fig. 16. Tangential section of a somewhat larger sporangium, the protoplasm is being cut up into irregular blocks.

Fig. 17. Tangential section of a sporangium, the irregular blocks of protoplasm are being cut up into spores, the nuclei are not well shown.

Fig. 18. Mature multinucleate spores.

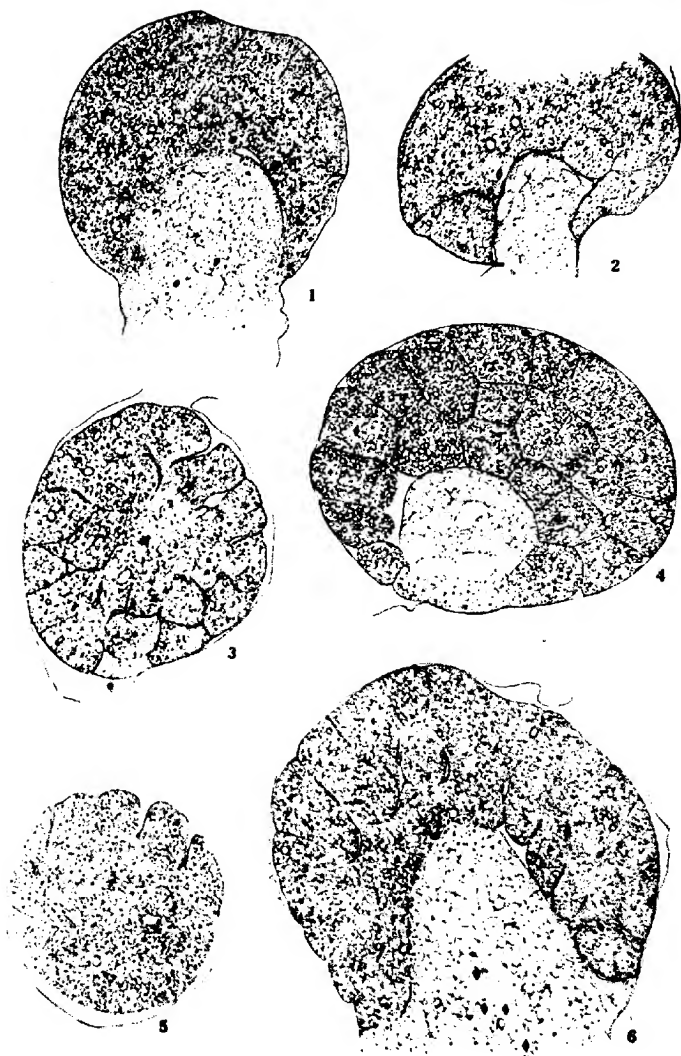
Mucor mucedo

Fig. 19. Median vertical section of a sporangium, columella-cleft nearly complete on one side but in the early stage on the other side.

Fig. 20. Outline drawing of a section of a sporangium showing cleavage of spore-plasm into relatively large protoplasmic blocks.

Fig. 21. Section of a sporangium showing spore-plasm cut up into uninucleate spore-initials.

Fig. 22. Outline drawing of a median vertical section of a small sporangium showing polyhedral spore initials.



SPORANGIUM GRANDE

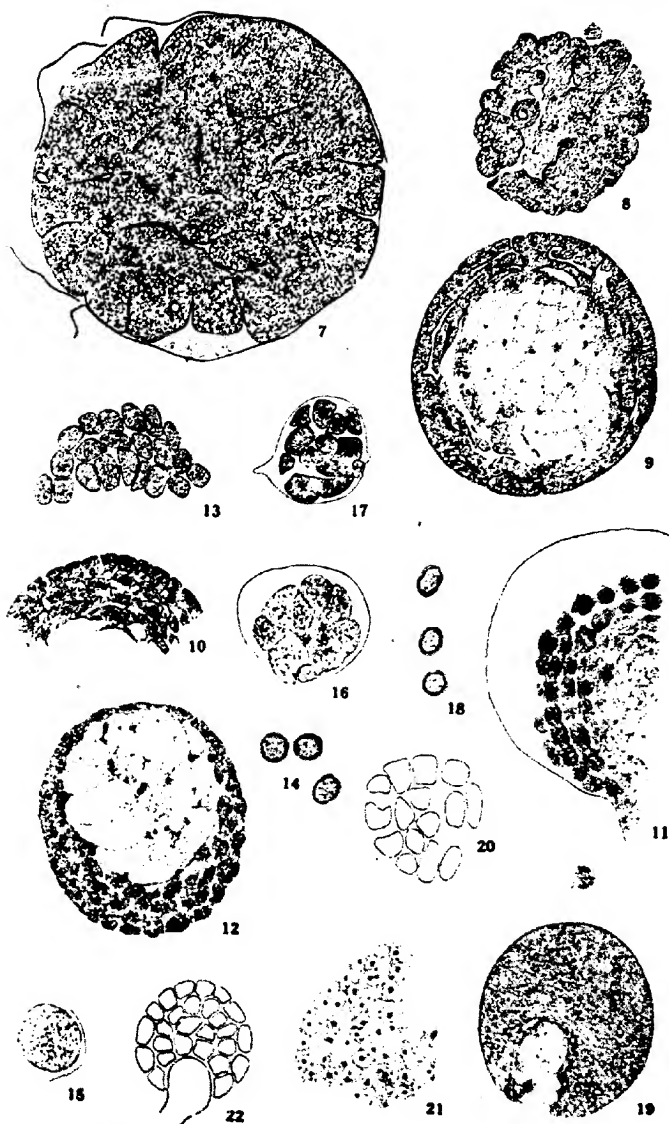


FIG. 7. *SPORODINIA GRANDIS*
FIG. 8-14. *CIRCINELLA MINOR*

FIG. 15-18. *MUCOR RACEMOSUS*
FIG. 19-22. *MUCOR MUCEDO*

